

ASSESSMENT OF AQUATIC FOOD WEB ALTERATIONS IN
THE PRESENCE OF THE EXOTIC CLAM, Corbicula
fluminea AND THE CICHLID, Oreochromis aureus

By

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The filter-feeding Asian clam, *Corbicula fluminea*, and omnivorous blue tilapia, *Oreochromis aureus*, have been established in Florida waters since the early 1960s. They are known for their ability to reach great abundance and to feed effectively on small particles such as detritus, phytoplankton, and microzooplankton. It was hypothesized that both exotic species may significantly alter the planktonic food web (first-order effect) as well as organisms that depend on smaller particles for food (second-order effect). In 37-liter laboratory microcosm experiments, *Corbicula* was able to reduce turbidity levels and bacterioplankton, phytoplankton (as chlorophyll-a), and

rotifer biomass significantly. Freed from fish predation, the planktonic structure of the water column shifted almost exclusively to larger cladocerans and copepods.

Once fish larvae have absorbed their nutritional yolk sac, after approximately seven days, they must immediately feed on microzooplankton to survive. In laboratory microcosms, a second-order effect from *Corbicula*'s filter-feeding was a reduction of useable food available in the water column. Because of this, fathead minnow (*Pimephales promelas*) larvae suffered significant mortality in microcosms containing *Corbicula*, presumably due to starvation.

Although each clam can filter approximately 600 mL - 800 mL hr⁻¹ of water, not all planktonic organisms are assimilated. *Corbicula* produce pseudofeces that encase whole algal cells and small rotifers. With the aid of a microbial technique based on reduction of 2(p-iodophenyl)-3-(p-nitrophenyl)-5(phenyl tetrazolium chloride) (INT), active cyanophytes, *Anabaena* and *Microcoleus*, were found in pseudofeces. This encased viable material may represent a valuable nutritional addition to benthic and pelagic organisms, as well as a nutrient source to the benthos.

The cornerstone assumption of whole lake biomanipulation experiments in temperate areas is that large

cladocerans and copepods will increase significantly if freed from fish predation. The increase in zooplankton abundance will be followed by oligotrophication, as filter-feeding zooplankton will significantly reduce algal biomass.

Three month-long experiments (depicting summer, winter, spring/fall) were run in twelve outdoor mesocosms, each containing 1420 L of water. As *Oreochromis* and *Corbicula* are efficient planktivores, it was hypothesized that the clams+fish mesocosms would consistently have lower algal biomass. In both fishless (control, clams) and fish-containing (fish, clams+fish) mesocosms, cladoceran and copepod biomass did indeed increase during the winter experiment, with significant phytoplankton reduction. During the spring and summer experiments, cladoceran and copepod biomass again increased, but phytoplankton increased as well. *Oreochromis* and *Corbicula*, separately or together, were not able to reduce algal biomass during warm ($>24^{\circ}\text{C}$) water periods. This also confirms that even with significant increases in cladoceran and copepods, these small-bodied Florida forms are not able to control algal biomass effectively. Thus, removing predaceous fish with the hope it would lead to oligotrophication is not effective in subtropical waters.

These experiments demonstrated that to achieve successful biomanipulation of waters in the subtropics with the goal of reducing algal biomass, the addition of a filter-feeding exotic clam (*Corbicula*) and phytophagous fish (*Oreochromis*) may be needed, contrary to what is shown in temperate systems.

CHAPTER 1 INTRODUCTION

Technological advancements in transportation have made it possible for plants and animals to be shipped from one continent to another in a matter of just a few hours or days. Plants and animals that historically were unable to survive a transoceanic crossing in a wooden sailboat that took weeks or months to reach its destination are now easily transported around the globe (Carlton 1989b). The movement and survival of these "nonindigenous" animals into "non-native" ecosystems has not been made without tremendous ecological alterations to native ecosystems (Yount 1990).

Nonindigenous or exotic species, are organisms that are able to enter an ecosystem beyond their historic range. These organisms are able to enter a foreign ecosystem through natural or human perturbations. Examples of natural perturbations such as climatic (wind dispersal, floods) or geological events (such as eliminating physical barriers by earthquakes) that have moved organisms outside their historic natural ranges are rare (Coblentz 1990). Examples of nonindigenous organisms that have become established

(successfully able to reproduce) within the last two centuries due to human perturbations brought about by urban development, agriculture, transoceanic shipping, interoceanic canals, and jet travel are numerous and alarming to most ecologists (Herbold and Moyle 1986).

A cold-water species from the South Atlantic Ocean, for example, would not be able to inhabit the North Atlantic because it is unable to travel across the thermal barrier that the equatorial waters presents (Royce 1984). Many riverine species are unable to expand into nearby hydrologic drainage basins because of their inability to withstand abrupt changes in both water temperature and salinity (Master 1990). Humans have eliminated these physico-chemical barriers by providing global transport of these organisms beyond their historic range and have made it possible for both marine and freshwater exotic species to threaten native ecosystems (Mooney and Drake 1986).

The most serious exotic species introductions have come about by deliberate transport of aquatic organisms from one place to another for aquarium use, aquaculture, and research (Devoe 1992). During this century, unintentional introductions of exotic zooplankton, invertebrates and larval fish have happened because of huge transoceanic

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tankers taking in bilge-water at a foreign port of origin and dumping this water into the waters of United States' ports before taking on cargo (Carlton 1985, Moyle 1991).

For years, population ecologists have described the mechanisms that are continually at work to determine the abundance and range that a particular species may reach (Colinvaux 1986). When a population begins to exceed its carrying capacity, factors such as food availability, disease, and predation will likely reduce the population size of the species (Watts 1971). An exotic species has few natural enemies in its new ecosystem, and the resident species are not adapted to this new species. Because of this and other reproductive (higher fecundity) and feeding (mouth brooding) strategies that generally give the exotic species an advantage over native residents (Balon 1986), the population of the successful biological invader may increase dramatically. In many instances, these increases tend to lead to a displacement of many of the native organisms (Kraemer 1979, Colinvaux 1986). The ecological effects of exotic aquatic organisms on native communities may be substantial primarily through (1) alteration of the native habitat; (2) introduction of exotic diseases and parasites into the native community; (3) hybridization with

the native species; (4) trophic alterations that can have detrimental cascading effects; and (5) spatial alterations.

The presence of exotic organisms and the financial and ecological ramifications of their presence are timely and relevant topics to Floridians (Schramm and Jirka 1989). Consider the possibility of exotic fish displacing native recreational fish important to Florida's economy; exotic plants costing Floridians millions of dollars in weed control to keep our waterways open; exotic reptiles that may feed on native bird eggs; *Casuarina* and *Melaleuca*, which continue to spread in the Everglades and threaten its watershed; and exotic birds that feed on the juice of Florida citrus.

In recent times (especially within the last 50 years), it has become impossible to conduct research and to address causes of environmental changes occurring in many aquatic ecosystems without factoring in the presence of exotic species (Laycock 1966, Master 1990). Many aquatic exotic organisms including plankton (Bowman et al. 1981, Burr 1988, Barnhisel 1991, Lehman 1993), gastropods (Berman and Carlton 1991), mollusks (McMahon 1983, Carlton 1989a, Mackie et al. 1989, Carlton and Rosenfield 1991), and fish (Drenner et al. 1987, Selgeby 1988) have become established and abundant in

U.S. rivers (McMahon 1982), lakes (Garton et al. 1993), and estuaries (Drake et al. 1989). Are observed water quality changes such as an increase in transparency in these water bodies related to changes in surrounding land use, or are they the result of biological changes within the water body itself (such as the new presence of a filter-feeding exotic species)? Do introduced species significantly alter the abundance and composition of trophic levels comprising food webs? If they do, is this necessarily a negative impact? It is the purpose of the current research to specifically address such questions.

This dissertation comprises seven chapters. By reviewing the literature and observing changes in planktonic community structure in aquaria containing *Corbicula*, seven hypotheses were developed that were addressed in my dissertation. Chapter 2 is a thorough review of the literature as it pertains to the ecological ramifications of exotic species in general (with some mention of *Oreochromis*), and the ecology and population dynamics of *Corbicula* in particular. Based upon review of the literature, development of hypotheses and the rationale for each are also presented in this chapter. I conducted controlled laboratory experiments under optimal conditions

(water temperature, substrate type, food availability) using 37-liter microcosms to further refine my seven hypotheses (Chapter 3).

Another purpose of the laboratory experiment was to design an outdoor mesocosm study where trophic level interactions could be assessed under a variety of physical and biological conditions. It is known from the literature that many estuarine filter-feeding macroinvertebrates possess the capability of significantly altering both the chemistry and biology of the overlying water column. Chapter 4 discusses how these chemical and biological changes affect fish eggs and larvae. Corbicula tend to "package" planktonic organisms in mucilaginous pseudofeces, thereby transporting food particles from the water column to the benthos. The fate of pseudofeces and its importance as a nutritional food source to other organisms is discussed in Chapter 5. Since these questions are addressed experimentally using controlled laboratory conditions, Chapter 6 assesses the significance of chemical and biological changes under more natural conditions using large, outdoor mesocosms.

As no experiment has the human or financial resources available to adequately address every unknown question

important to a particular topic, Chapter 7 summarizes what⁷
has been learned from the results presented in this
dissertation and discusses future research needs.

CHAPTER 2 LITERATURE REVIEW AND DEVELOPMENT OF HYPOTHESES

Introduction

Assessment of control mechanisms of planktonic community structure by benthic organisms is still relatively rare in limnology, although study in this area has received considerable attention in intertidal and estuarine research (Cloern 1982). Marine ecologists have begun to realize that benthic communities can alter the composition and abundance of pelagic organisms significantly. As exotic species may dominate areas in which they have become established, they have become a significant part of the biota in many water bodies and warrant attention (Drake et al. 1989).

The exotic filter-feeding clam *Corbicula* and planktivorous fish *Oreochromis* dominate many Florida lakes (Brenner et al. 1991), and rivers (Heard 1966, Gottfried et al. 1982). It is important to assess their impact on the aquatic food web. A review of the literature of the general ecological ramifications of a variety of common aquatic and marine exotics is presented. This review is intended to (a) discuss examples of the impact of aquatic organisms on

indigenous species and water quality; (b) present a historical and zoogeographical account of the Asian clam with some reference of the exotic cichlid; and (c) summarize the ecology and impact of *Corbicula*.

The Importance of Exotic Fish on the
Planktonic Structure of the Water Column

Most traditional schools of thought in limnology believe that a water body is primarily influenced by a "bottom-up control" where nutrients and light control net primary production in the water column, and hence, the rest of the food web (Wetzel 1983, Valiela 1991). Constraints are set primarily by the availability of phosphorus in freshwater systems in relation to the amount of nutrient uptake by phytoplankton cells.

With the introduction of exotic organisms, many limnologists are now recognizing that food web structure may be more influenced by negative "top-down effects" (Shapiro and Wright 1984). Bottom-up control is a positive relationship because if you add nutrients, you expect an increase in the abundance of phytoplankton and zooplankton (Wetzel 1983). A top-down effect is considered a negative response because adding a voracious predator would tend to decrease the overall abundance of planktonic organisms (Black and Harrison 1988). The negative consequences of

exotic predators on indigenous species are of special concern to the public as well as ecologists.

Exotic planktivorous fish cause negative top-down effects on zooplankton (Cramer and Marzolf 1970, O'Brien 1979, Drenner et al. 1984) and algae (Porter 1976, Lehman and Caceres 1993). Planktivory may directly change zooplankton and phytoplankton size structure and so indirectly affect both nutrient regeneration by zooplankton and the rate of nutrient uptake by phytoplankton (Novales-Flamarique et al. 1993). The ability of a particular fish or zooplankter to restructure the food web significantly is dependent upon the foraging habit of both organisms as well as their susceptibility to predation by other organisms (Schoener 1989).

Vinyard et al. (1988) demonstrated in outdoor mesocosm experiments that the exotic planktivores *Tilapia galilaea* and *O. aureus* were both able to suppress crustaceans and rotifers. When water temperatures rose in the mesocosms, the presence of *O. aureus* actually led to a significant increase in small-celled (nanoplankton) algal abundance. Cailteux et al. (1992) found that *O. aureus* decreased diatom populations in the fall and winter, chlorophytes in the spring, and cyanophytes in the summer in Florida lakes.

As with mollusks, exotic planktivorous fish alter the chemistry of the water column through their movements (resuspends sediment) and respiration (increases ammonia). Exotic mollusks tend to increase the concentrations of macronutrients in the water column (Asmus and Asmus 1991), but phytoplankton populations do not increase because their numbers can be suppressed by the efficient filter-feeding of the mollusks. Although many exotic fish also tend to increase macronutrient concentrations in the water column due to increased feces and resuspension of nutrient-rich sediment (Drenner et al. 1984, Mooney and Drake 1986), phytoplankton populations remain generally stable because their numbers are suppressed by pump-feeding exotic fish such as *Oreochromis* (Drenner et al. 1987).

The Importance of Exotic Benthic Filter-Feeders
on the Structure of the Overlying Water Column

Efficient capturing of plankton by filter-feeding bivalves can have a significant effect on water chemistry and food web structure of the overlying water column. An increase in macronutrient concentrations can generally be expected when a large community of respiring bivalves is present (Asmus and Asmus 1991). Whether or not this increase in available nutrients can lead to an increase in algal biomass (chlorophyll-*a*) through photosynthesis is

dependent on the grazing pressure of the filter-feeding benthos on phytoplankton (Lauritsen 1986b).

Because shallow tidal waters bring planktonic and larval organisms on a semi-diurnal or diurnal basis into areas with significant filter-feeding epifaunal/inafaunal populations, benthic-pelagic coupling in estuarine and intertidal areas has received considerable attention. Asmus and Asmus (1991) demonstrated that intertidal blue mussels (*Mytilus edulis*) filter and retain particles as small as 4 μm . Carlson et al. (1984) showed that *M. edulis* retain plankton cells as large as 35 μm - 50 μm (dinoflagellates and diatoms). Because of the wide range in particle retention by the mussel bed, phytoplankton, dinoflagellates, and diatoms (from picoplankton to microplankton) abundance were all reduced.

San Francisco Bay receives the bulk of the city's sewage effluent. As there are no obvious light, temperature, turbidity or nutrient limiting conditions present and the zooplankton population is small (Officer et al. 1982), the bay should function as a large eutrophic lake (Thompson 1992). With low grazing pressure and high nutrients, substantial seasonal phytoplankton blooms should characterize San Francisco Bay. This, however, is not the

case as the benthos of San Francisco Bay is dominated by abundant large exotic filter-feeders (clams and mussels) and suspension-feeders, including an array of polychaetes (Nichols and Thompson 1985a). Because numerous exotic mollusks have established (Figure 1) over the past 100 years (Table 1), it has been postulated that these abundant filter-feeders suppress phytoplankton populations (Officer et al. (1982), Nichols and Thompson (1985b), Nichols and Pamatmat (1988), and Alpine and Cloern (1992).

In the 1970's, the introduction of isopods (Rotramel 1972) and large copepods (Orsi et al. 1983), presumably from the ballast water of transoceanic ships (Carlton 1985, 1987), occurred in nearby estuaries. These planktonic exotic organisms seemingly have displaced the native copepod, *Eurytemora affinis* (Figure 2), and also may have caused the decline of rotifers and cladocerans as well (Alpine and Cloern 1992). With the loss of preferred phytoplankton, rotifers, and copepods, the larval abundance of striped bass (*Morone saxatilis*) has been reduced (Carlton 1989a).

In 1986, the Chinese clam, *Potamocorbula amurensis*, was first discovered in the northern part of the bay. This clam

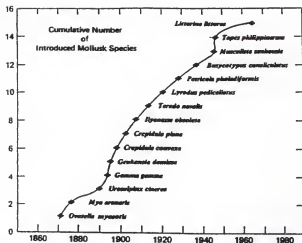


Figure 1. The steady rise in the number of mollusks introduced into San Francisco Bay (from Monroe and Kelley 1992).

Table 1. Chronology of introduction of exotic mollusks into San Francisco Bay in which they were first described (from Monroe and Kelley 1992).

<i>Mytilus edulis</i>	Native
<i>Macoma balthica</i>	Native (?)
<i>Ovatella myosotis</i>	1871
<i>Mya arenaria</i>	1874
<i>Urosalpinx cinerea</i>	1890
<i>Gemma gemma</i>	1893
<i>Ischadium demissum</i>	1894
<i>Cepidula convexa</i>	1898
<i>Crepidula plana</i>	1901
<i>Iyanassa obsoleta</i>	1907
<i>Teredo navalis</i>	1913
<i>Lyrodus pedicellatus</i>	1920
<i>Petricola pholadiformis</i>	1927
<i>Busycotypus canaliculatus</i>	1938
<i>Musculus senhousia</i>	1945
<i>Corbicula fluminea</i>	1946
<i>Tapes japonica</i>	1946
<i>Littorina littorea</i>	1968
<i>Theora fragilis</i>	1982

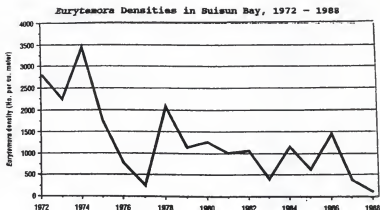


Figure 2. Decrease of the native *Eurytemora affinis* after the introduction of exotic copepods via ballast water (from Monroe and Kelley 1992).

has spread quickly throughout the bay (Thompson et al. 1992) and has displaced many of the benthic organisms (Nichols et al. 1990). With densities of up to 25,000/m², *Potamocorbula* have displaced many indigenous mollusks (Figure 3). By retaining large amounts of bacterioplankton and phytoplankton (Werner and Hollibaugh 1993), the phytoplankton biomass maximum usually occurring during the summer months in the bay has been reduced ten-fold by exotic filter-feeders (Herbold et al. 1992).

The successful establishment of *Corbicula* has somewhat changed the way we view freshwater benthic-pelagic coupling. The invasion of this bivalve has also forced us into examining food web interactions more carefully (Lehman and Caceres 1993). As soon as researchers began documenting the densities that *Corbicula* had obtained in shallow water environments and the amount of water that this bivalve can filter, it seemed logical that this exotic clam could alter the community structure of the overlying water column.

Buttner (1986) found measurable improvement in water quality (greater dissolved oxygen and net production and less turbidity) in channel catfish (*Ictalurus punctatus*) ponds that contained *Corbicula* over those that did not. As expected, *Corbicula* was able to reduce suspended solids in

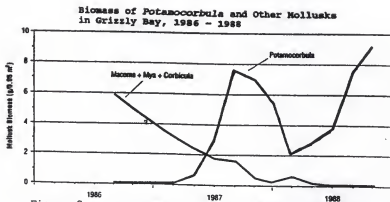


Figure 3. The increase in the biomass of the exotic *Potamocorbula* and the significant decrease in the biomass of other resident mollusks (from Monroe and Kelley 1992)

these aquacultural areas and was viewed as an effective biofilter (Buttner 1986). Because of *Corbicula*'s filtering capability, changes in plankton abundance, composition, and diversity were clearly noted. As phytoplankton was suppressed, water clarity throughout the Bay increased significantly (Thompson et al. 1992).

Cohen et al. (1984) noticed that a significant phytoplankton sag existed along a stretch of the Potomac River during the summers of 1980 and 1981. It was discovered that the benthic community within the area of the phytoplankton sag contained very dense beds of *Corbicula* ($1,467/\text{m}^2$). Just downstream of the mollusk bed, chlorophyll concentrations were 60% less than those found immediately upstream. The researchers hypothesized that the 60% reduction in phytoplankton biomass downstream of the mollusk bed was related to *Corbicula* and retention of these particles (Cohen et al. 1984).

Water transparency in Lake Erie doubled between the summers of 1988 and 1989 (Reeders and de Vaate 1990). The significant decrease in phytoplankton abundance and suspended solid levels has been attributed directly to the arrival of the exotic filter-feeding zebra mussel (Wu and Culver 1991). The first-order (direct) impact of reducing

phytoplankton and microzooplankton populations and the second-order (indirect) impact of losing breeding substrate to the exotic mussel are expected to alter egg deposition and overall recruitment success of Great Lakes fishes (Roberts 1990).

Corbicula is a non-selective filter-feeder (Lauritsen 1986b). This exotic clam filters and retains both chlorophytes and cyanophytes equally well. Algal composition did not change filtration rates in laboratory experiments. Numerous field and laboratory experiments have shown that *Corbicula* can greatly reduce phytoplankton and turbidity levels (Lauritsen 1986b), thereby increasing water transparency. MacIsaac et al. (1991) stated that incidental predation on small-bodied molluscan larvae and rotifers by *D. polymorpha* in Lake Erie may reduce food available to larger planktonic taxa such as *Bosmina* and *Scapholeberis*. Being indiscriminant filter-feeders, it is clear that both the Asian clam (*Corbicula*) and Caspian zebra mussel (*Dreissena*) can significantly alter the planktonic composition of the overlying water column.

The Influence of Exotic Mollusks on Nutrient Levels and Regeneration

Corbicula have the ability to filter much larger volumes of water than most indigenous freshwater mollusks

(Leff et al. 1990). As with any mollusk, food particles taken into the incurrent siphon can either be assimilated, respired, or released as pseudofeces. The net growth efficiency of *Corbicula* can be higher than in any other species of freshwater or marine bivalve for which similar values have been reported (Morton 1977, McMahon 1983, Lauritsen 1986a, Way et al. 1990).

In grazing experiments involving *Corbicula* (McMahon 1979) nutrients increased in many laboratory microcosm experiments (Hoagland 1986, Lauritsen and Mozley 1989). Filter-feeding bivalve mollusks may be an important factor in nutrient cycling in aquatic habitats, both indirectly through burrowing and sediment reworking, and directly, through excretion of metabolites (Purchon 1977). Because of their abundance, *Corbicula* may release high levels of ammonia (NH_3) and phosphate (PO_4) to the water column (Lauritsen and Mozley 1989). Both of these excreted nutrients are reactive biologically and can be rapidly absorbed by phytoplankton (Sackheim 1991).

Although an increase in biologically reactive dissolved macronutrient levels may be expected from dense mollusk beds (Barnes 1974), it is unclear whether these organisms enhance or accelerate nutrient remineralization by bacterioplankton

or phytoplankton. The filtration rate of bivalves is usually very dependent on water temperature and seston quality (Way et al. 1990). The filtration rate of bivalves generally increases with increasing temperature (Lauritsen 1986a). Whether or not nutrient excretion is balanced by removal of phytoplankton through filter-feeding appears to be the deciding factor whether or not nutrient enrichment of the water column can be expected.

Carlson et al. (1984) noted that filter-feeding and nutrient excretion were highest during spring and summer in mudflat communities in the Gulf of Maine. Although nutrient levels increased during this period through increased respiratory activity, phytoplankton (chlorophyll-a) decreased significantly. Officer et al. (1982) and Cloern (1982) made similar observations in San Francisco Bay. Although Asmus and Asmus (1991) measured increased ammonium (NH_4) from a dense mussel (*M. edulis*) population in an experimental flume in the North Sea, phytoplankton concentrations were reduced by approximately 37% inside the flume. Sullivan et al. (1991) found that phytoplankton abundance was reduced in the presence of abundant filter-feeding bivalves in Narragansett Bay (Rhode Island) regardless of whether the water column was nutrient enriched or limited.

Several laboratory and field experiments have reported high water-column nutrient concentrations where large filter-feeding bivalve communities dominate the benthos. It has been postulated that an increase in important macronutrients in the water column associated with respiring bivalves may actually increase primary productivity by available phytoplankton (Asmus and Asmus 1991). While this certainly appears logical, elevated nutrient concentrations where abundant bivalve populations are found seem to be offset by increased benthic grazing of phytoplankton.

Interspecific Competition of Corbicula With
Other Mollusks in Lotic Environments

Opportunities to investigate interspecific competition increased substantially during the 1900's with the continuing introduction of exotic species into new geographical areas (Yount 1990). The fact that *Corbicula* has spread across the country at the same time that native populations of river mollusks has dwindled (Drake et al. 1989) certainly suggests that *Corbicula* have successfully outcompeted many native species.

Competition occurs whenever a valuable resource (food or space) is sought by a number of different plants or animals (Colinvaux 1986). Ecologists have long accepted the idea that animal populations must share resources in order

to avoid loss of energy due to competition. If competition is limited, more energy can be directed towards reproduction and fitness (Watts 1971, Colinvaux 1986). However, competition for food and space is usually keen among relatively non-motile organisms such as mollusks and slow-moving gastropods (Brenchley and Carlton 1983). The life history and adaptive characteristics of any organism usually determines their competitive success in reproducing and extending their geographic range. Many exotic plants and animals have been very successful in rapidly extending their geographic range from their original point of entry in the United States. *Corbicula*, first discovered in the Pacific Northwest in 1938, was found in Florida waters less than 25 years later (Heard 1966, McMahon 1983).

In a stable aquatic environment, one might expect that benthic assemblages in rivers would include an arthropod component (usually insect larvae) and a mollusk component (usually bivalves and/or gastropods) (Wetzel 1983, Moss 1992). With *Corbicula* populations reaching into the 1,000s/m² in California (McMahon 1983, Foe and Knight 1985) to the 10,000s/m² in Arkansas (McMahon 1983), many lake bottoms in these areas lack the arthropod component. *Corbicula* seem to be able to outcompete indigenous benthic

organisms where they are forced to share the same food and space.

Corbicula are either overwhelmingly dominant in numbers in perturbed areas or rare as a benthic component in relatively pristine riverine systems (Boozer and Murkes 1979, Kraemer 1979). From an ecological standpoint, this suggests that *Corbicula* are more highly opportunistic than they are competitively superior to indigenous mollusks. In heavily managed and perturbed aquatic ecosystems where conditions may change rapidly, high fecundity, release of highly motile juveniles, and short life span of *Corbicula* would be competitive advantages. In stable areas where the benthic component may have evolved over millions of years, the opportunistic characteristics of *Corbicula* may be of no competitive advantage over large indigenous mussels where environmental stability and minimum competition among benthic organisms exist (Kraemer 1979).

Kraemer (1979) conducted field monitoring (Ponar grabs) along a 150-kilometer long stretch of the Arkansas and Buffalo Rivers to assess competition between *Corbicula* and *Lampsilis*. The Arkansas River Navigation System is a highly "managed" lotic system because of boat traffic, dredging, development, and recreational uses. In contrast, the

Buffalo River is a relatively wild "unmanaged" lotic system in northern Arkansas where conditions are relatively stable. If *Corbicula* were more of an opportunistic colonizer than a superior competitor, one would expect that its dominance as a benthic component of each river system would be significantly different.

In the Buffalo River, the benthic community consisted of 35 genera of midge larvae (Insecta: Chironomidae) along with a highly diverse assemblage of indigenous species of mollusks (especially the unionid river mussels). Although *Corbicula* is present, it does not seem to exhibit the high biomass found in perturbed sites. The densities of *Corbicula* in heavily managed canals and lotic systems are legendary (McMahon 1983). In areas where extensive management and perturbation alter lotic systems such as canals, dams, bank stabilization projects along rivers and dredged navigation channels, *Corbicula* tend to either dominate or displace the benthic molluscan component (Kraemer 1979, McMahon 1983).

Whether or not exotic mollusks such as the Asian clam (*Corbicula*) or Caspian zebra mussel (*Dreissena*) will expand their current ranges appears largely to rest with their ability to be opportunistic colonizers in managed or

perturbed habitats. Unfortunately for indigenous organisms, the amount of dredging, channel stabilization and urbanization of both lentic and lotic systems will likely continue to increase in the future. Because of the opportunism exhibited by both of these mollusks, their range extension into aquatic systems not currently colonized appears likely.

Predation of Aquatic Organisms on Corbicula

It has been hypothesized that the appearance of large numbers of exotic organisms may actually provide a valuable food source for a number of indigenous species or a much needed new commercially or recreationally important animal. Unfortunately, all purposeful introductions have been with good intentions such as enhancing recreational fisheries and adding a food source (Balon and Bruton 1986, Carlton 1989a). These objectives have occasionally been achieved (Mann et al. 1991), but in the majority of cases negative ecological impacts of introducing an organism into the environment occurred (Sinderman 1986, Coblenz 1990, Kaufman 1992). As the exotic organism becomes established, it is hoped that the indigenous species will recognize the biological invader as a welcome food source (McMahon 1983).

Corbicula cannot be controlled by biocides and molluscicides because it closes its valves tightly to isolate its tissues from the toxic agents for several days or even weeks (McMahon 1983, Reinholtz 1986). Because of this, population control centers on density-dependent factors such as interspecific competition and disease, as well as predation by indigenous organisms (McMahon 1983). Although predation or parasitism may limit *Corbicula* densities in some environments, these impacts have just recently been subjected to a detailed and rigorous assessment. Research in these areas has increased in recent years in order to document the use of *Corbicula* as a primary food source for many indigenous organisms.

The major predators of young and adult *Corbicula* are fish (Sickel 1986). Although the comparatively heavy strong shells of adult *Corbicula* appear to preclude significant predation (McMahon 1983, Sickel 1986), the list of animals preying on it is constantly expanding. Young *Corbicula* up to 5 mm have been found in the gut of such important freshwater fish as the redear sunfish (*Lepomis microlophus*), bluegill (*Lepomis macrochirus*), freshwater drum (*Aplodinotus grunniens*) blue catfish (*Ictalurus furcatus*), and channel catfish (*Ictalurus punctatus*), suggesting that these fish

consume young clams regularly (McMahon 1983, Sickel 1986). Recently, *Corbicula* fragments have been found in the gut of the endangered shortnose sturgeon (*Acipenser brevirostrum*) that inhabits some of the rivers along Florida's Gulf coast, and crayfish (*Procambarus clarkii* and *Cambarus bartonii*) have been shown to prey upon *Corbicula* in the 6 mm - 9 mm size range in laboratory microcosm experiments (Sickel 1986).

Transient predators such as wild ducks and raccoons have been shown to consume large numbers of adult *Corbicula* (McMahon 1983, Sickel 1986). Such predation does not appear to reduce *Corbicula* densities significantly in most North American drainage systems. The growing list of documented predators does, however, suggest that *Corbicula* may contribute to several mollusk-eating fish and waterfowl in the future. *Corbicula's* presence may become an important food source in areas where they are abundant.

Development of Hypotheses

Based on review of the literature, the following hypotheses were formulated for this dissertation:

H₁: The presence of filter-feeding *Corbicula* will significantly decrease dissolved oxygen levels and increase dissolved nutrient concentrations (particularly in the form of ammonium) over time.

H₂: The presence of filter-feeding *Corbicula* will significantly decrease turbidity levels and chlorophyll-a over time.

H₃: The presence of filter-feeding *Corbicula* and *Oreochromis* will significantly decrease total bacterial levels over time.

H₄: The presence of filter-feeding *Corbicula* and *Oreochromis* will significantly increase the amount of viable pseudofeces that accumulates on the benthos over time.

H₅: There will be a significant decrease in small-bodied rotifers and an increase in large-bodied cladocerans and copepods over time.

H₆: There will be significant mortality among fish larvae in enclosures containing *Corbicula*.

H₇: There will be significant "improvements" in water quality in enclosures containing *Corbicula*.

CHAPTER 3
ASSESSING NUTRIENT AND PLANKTON CHANGES IN LABORATORY
MICROCOSMS IN THE PRESENCE OF Corbicula fluminea

Introduction

Corbicula reach densities of 1000s/m² (Gardner et al. 1976,) with each animal capable of filtering between 400 mL and 950 mL of water per hour (McMahon 1983), suggesting that it may be capable of significantly changing the physical, chemical and biological properties of water bodies. It was the purpose of this experiment to assess changes in macronutrient levels at the beginning and end of the experiment and quantify what impact, if any, *Corbicula* might have on plankton community structure. Additionally, the potential impacts to higher trophic levels by *Corbicula* altering the base of the food chain (phytoplankton and microzooplankton) will be discussed.

A laboratory experiment using 37-liter microcosms under *Corbicula*'s optimal water temperature (around 24°C) where presumably food would never be limiting (hypereutrophic water) was undertaken. Results of this experiment were statistically compared to note microcosm water column

changes in the presence/absence of *Corbicula* and were used to design an outdoor experiment using large mesocosms (Chapter 6).

Methods

Corbicula of various sizes and life stages were collected by Ponar grab, rakes and SCUBA from a small tributary (New River) of the Santa Fe River in north Florida (Bradford County). To minimize stress, animals were transported to the University of Florida (UF) in approximately 4.0 liters of river water along with the sandy coarse substratum that these infaunal organisms inhabited.

In a stable environmental chamber at UF, coarse sand, clams, and river water were placed in a 113-liter microcosm. Inside the chamber, automatic timers produced 12 hours of light and 12 hours of dark daily. As the clams were collected in early September, this light/dark scenario represented the approximate natural photoperiod found in north Florida at this time of year. To avoid stress to the animals through sudden temperature changes, the water temperature of the microcosms was set at the same 24°C found in the New River. Over the next 48 hours, approximately 1.5 liters of hypereutrophic water (representing food) from

nearby Lake Alice was added every 12 hours. Care was taken to acclimate the clams to the new laboratory conditions in order to reduce stress sometimes associated with microcosm experiments (Foe and Knight 1986).

Each of the 37-liter microcosms was filled with 4-cm of tripled-rinsed builder's sand and hypereutrophic lake water. Each microcosm was aerated in order to reduce settling of phytoplankton and detritus in the microcosm, increasing the ability of filter-feeding *Corbicula* to extract the particles from the water column. The experimental design consisted of three microcosms each for (a) control (no clams); (b) 30 clams, simulating a density of approximately 1310 m^2 in a 2 meter deep water column; and (c) 60 clams, simulating a density of approximately 2620 m^2 in a 2 meter deep water column.

These clam densities and water column depth were chosen to mimic conditions found in some of Florida's eutrophic lakes, including Lake Okeechobee (Heard 1966, Gardner et al. 1976, Jenkinson 1979, Branson et al. 1989). Furthermore, these conditions allowed comparison with past experiments from temperate areas (Cohen et al. 1984, Lauritsen and Mozley 1989).

Dissolved oxygen and water temperature were monitored daily. These parameters are very important, as *Corbicula* can become severely stressed under hypoxic conditions (McMahon 1979, Foe and Knight 1986). As shown in previous filtration studies (McMahon 1983, Lauritsen 1986b, Beaver et al. 1991), the maximum filtering rate of *Corbicula* is usually achieved between 20°C - 24°C (Mattice 1979, Way 1990). With aerated water and a constant optimum water temperature, the filter-feeding clams were expected to filter large volumes of water over the eight-day (192-hour) experiment.

Triplicate water samples were taken from the center of each microcosm at 0, 12, 24, 48, 72, 96, 120, 144, 168, and 192 hours. A wide-mouth 200 mL Nalgene bottle was sent to the bottom of each microcosm and slowly lifted to the surface. By utilizing this collection method, it was assumed that the water sample integrated the microcosm water column. Macronutrient (forms of nitrogen and phosphorus) samples were taken at the beginning (0 hours) and end (192 hours) of the experiment and analyzed utilizing a Technicon autoanalyzer (APHA methods 1988). Turbidity (NTUs) was estimated utilizing a Spectronic 20 spectrophotometer.

Bacterial abundance (averaging triplicate samples of 10 mL each) was estimated by using the acridine orange epifluorescence direct-count method (Hobbie et al. 1977). Chlorophyll-a concentrations were calculated using the trichromatic acetone method (APHA 1988).

Zooplankton samples (500 mL) were passed through a 41-um mesh net (Wetzel and Likens 1991) and immediately preserved with 5.5 mL of Lugol's solution (Steedman 1976) to aid in identification. From a 100 mL agitated sample, 1 mL was pipetted off and placed into a Sedgewick-Rafter chamber. Zooplankton abundance was estimated by directly counting 5 subsamples at 200x using an inverted microscope (APHA 1988, Wetzel and Likens 1991) and averaged out.

Fifty individual specimens were poured onto a previously weighed glass fiber filter. The sample was sucked dry by vacuum filtration. The filter was heat dried in an oven at 60°C for 24 hours, which was transferred to a desiccator, and allowed to cool for 1-3 hours. Dry weight (dw) biomass (mg dw/m³) of the specimens were estimated, using a sensitive electrobalance (Steedman 1976, Wetzel and Likens 1991). This procedure was repeated an additional four times and the results were averaged out.

Results and Discussion

Macronutrients

Based on the formulae and descriptions of Jorgensen (1966), Coughlan (1969), Lauritsen (1986a), Sanderson and Wassersug (1990), Way et al. (1990), and Cole et al. (1992), it was assumed that *Corbicula* in the 1310 clams/m² microcosms (herein referred to as clam 1x) filtered approximately 400 mL hr/clam and 650 mL hr/clam in the 2620 clams/m² microcosms (herein referred to as clam 2x). Normally, density-dependent stress in the clam 2x microcosm would cause filtration rates to actually be less than those found in the less dense clam 1x microcosms. As densities in the clam 2x microcosms are less than those found in many other areas in the southeastern U.S. (Lauritsen 1986b), it was felt that filtering ability was not inhibited at this density. Nitrite/nitrate concentrations increased slightly in both the control and clam microcosms (Figures 11a, 11b, 11c). While ammonia increased in all microcosms, the increase was significantly higher in the microcosms containing *Corbicula* (Figure 11b, 11c). With high filtration rates, it appears that this increase in ammonia is a byproduct of the respiring clams.

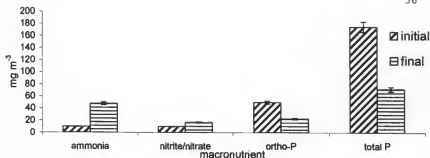


Figure 4a. Changes in macronutrient concentrations in control microcosms (no clams)

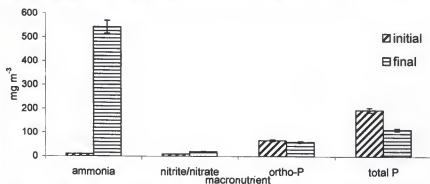


Figure 4b. Changes in macronutrient concentrations in microcosms containing 1310 clams/m²



Figure 4c. Changes in macronutrient concentrations in microcosms containing 2620 clams/m²

NOTE: Error bars represent 95% confidence intervals in all figures.

The released ammonia could be readily utilized by phytoplankton if no other nutrient compound was to become limiting over the course of the experiment. For example, Doering et al. (1986) measured a doubling of phytoplankton production in mesocosms by introducing *Mercenaria mercenaria* into the system. In comparison to live phytoplankton settling out of the water column by sedimentation, phytoplankton consumed by *Corbicula* may actually be recycled faster back into the water column through digestion processes (Ball and Arthur 1981, Lauritsen and Mozley 1989). Remineralization by filter-feeders is high (Dame and Dankers 1988, Asmus and Asmus 1991), and nutrients are quickly taken up by phytoplankton (Kiorboe and Mohlenberg 1981, Carlson et al. 1984). *Corbicula* therefore may actually stimulate phytoplankton through their high filtration rates.

Phosphorus (total and orthophosphate) decreased in both the control and clam 1x mesocosms but slightly increased in the clam 2x microcosm. Phosphorus is usually released into the water column by inefficient filter-feeding. Because overall phosphorus concentrations generally remained stable or slightly decreased (as opposed to ammonia) feeding by herbaceous zooplankton and mollusks seemed to be efficient.

At first, the idea that mollusks may actually stimulate phytoplankton seems a contradiction as it has been shown in several studies (Dresler and Cory 1980, Cohen et al. 1984, Phelps 1994) that *Corbicula* significantly reduces phytoplankton standing crop. Can phytoplankton standing crop actually increase due to the greater remineralized macronutrient concentrations in the water column produced by respiring *Corbicula*? This can only happen if sufficient phytoplankters are available to take advantage of the increased nutrient levels. This possibility will be discussed later in this chapter when the impact of *Corbicula* on phytoplankton is assessed.

Turbidity

The impact of *Corbicula* filter-feeding on small particles in the water column (suspended detritus and picoplankton) was dramatic (Figure 5). The greatest impacts were observed within the first twelve hours of the experiment. While not exhibiting a feeding saturation curve, *Corbicula* first filtered and removed particles from the water column quickly, with feeding gradually slowing down over time as its gut becomes full.

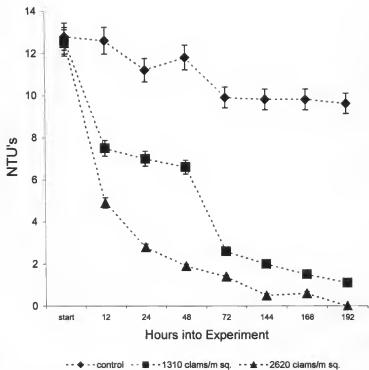


Figure 5. Changes in overall turbidity (NTU's) over a 192 hour experiment. Error bars represent 95% confidence intervals.

Overall turbidity (expressed as NTU's) was rapidly reduced by an average of 40% within the first twelve hours in the clam 1x microcosms and 61% in the clam 2x microcosms. After 192 hours, turbidity in the control microcosms had been reduced by 25% (likely from phytoplankton settling and zooplankton grazing). This is significantly less than the clam 1x ($p=0.008$) and clam 2x ($p=0.001$) microcosms, which experienced reductions of 91% and 100%, respectfully. There was no significant difference ($p=0.48$) between turbidity levels in the clam 1x and clam 2x microcosms. A doubling of clam biomass in the clam 2x did not translate into reducing water column turbidity twice as fast as that in the clam 1x microcosms. Stockner (1988) found physiological stress in clams associated with overcrowding and competition for food. Phelps (1994) hypothesized that not all clams in a particular reach of the Potomac River were filter-feeding all the time, therefore a simple linear relationship cannot be made between clam abundance and rate that turbidity levels can expected to be lowered.

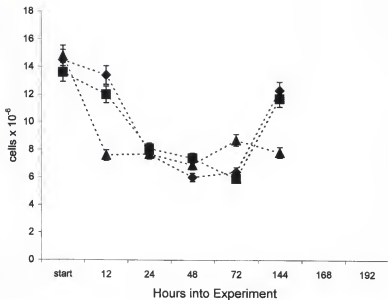
Bacterioplankton

Heterotrophic bacterioplankton occur in the water column as single cells or small colonies (Scavia et al.

1986). Many bacteria are commonly attached to either detritus or live organisms such as phytoplankton and protozoans (Mann 1988). Bacteria may be more readily utilized as a nutrition source by filter-feeding mollusks such as *Corbicula* or large zooplankton grazers such as copepods if they are attached to something rather than free-living (Schoenberg and MacCubbin 1985). Although difficult for larger organisms to filter and retain if not found in colonies, picoplankton (organisms generally defined as being <10 μm in size) such as bacterioplankton represent a very important food source to a wide variety of suspension-feeding and filter-feeding organisms (Stockner 1988, Gee 1991).

As just described, significant reductions in the amount of organic detrital particles (turbidity) occurred in microcosms due to filter-feeding *Corbicula*. Because of the loss of substrate that bacteria could attach to, it was thought that overall bacteria numbers would be reduced.

Within the first 12 hours of the experiment, bacterial abundance in microcosms declined (Figure 6), 7% in the control, 12% in the clam 1x, but 48% in the clam 2x microcosms. After 24 hours, no significant difference in



--◆-- control --■-- 1310 clams/m sq. --▲-- 2620 clams/m sq.

Figure 6. Changes in microcosm bacteria abundance. Error bars represent 95% confidence intervals.

bacterioplankton levels existed in any of the microcosms. This trend continued over the next 48 hours, until unexpectedly, bacteria abundance increased in the both the control and clam 1x microcosms while the clam 2x microcosms saw a continued decline (15%). It is possible that at this point in the experiment, filter-feeding *Corbicula* and predatory copepods had already greatly reduced those organisms such as predatory ciliated protozoans and rotifers that feed on smaller picoplankton, bacteria and detrital particles (Carlson et al. 1984). Freed from the predation, it seems reasonable to expect that bacterial numbers may be expected to increase over time (Valiela 1991, Wu and Culver 1991) as the number of predators decreases.

After 144 hours, no significance difference was found between the control and clam 1x microcosms ($p=0.325$), but a significant difference did exist between the control and clam 2x microcosms ($p=0.003$). The significant difference was only seen in the clam 2x microcosms at the beginning (12 hours) and end (144 hours) of the experiment. However, it should be noted that no significant differences existed between the microcosms during at least half of the experiment (24-72 hours).

Besides *Corbicula*, it is suggested that the presence of a wide variety of suspension-feeding (Kiorboe and Mohlenberg 1981) and filter-feeding zooplankton such as rotifers (Neil 1984), cladocerans (Gilwicz 1990), and copepods (Wu and Culver 1991) can contribute to the decline of bacterioplankton through grazing (Kalff 1986, Dawidowicz 1990). Schoenberg and MacCubbin (1985) found that bacterial numbers in the presence of large, efficient, suspension-feeding and filter-feeding organisms in shallow water intertidal estuaries were lower than that found in adjacent waters. Previous studies by Fenchel (1974), Mann (1988), Stockner (1988), Mann et al. (1991) and Sullivan et al. (1991) concluded that mollusks, sponges and tunicates exert a considerable influence on small particles (bacteria, phytoplankton, zooplankton, and fish larvae) in the overlying water column.

Chlorophyll-a

Chlorophyll-a concentrations dramatically declined within the first twelve hours (Figure 7). Levels declined in the control microcosms by an average of only 1% (from 104 to 103 mg m^{-3}) while the clam microcosms experienced chlorophyll-a level declines of an average of 42% in the

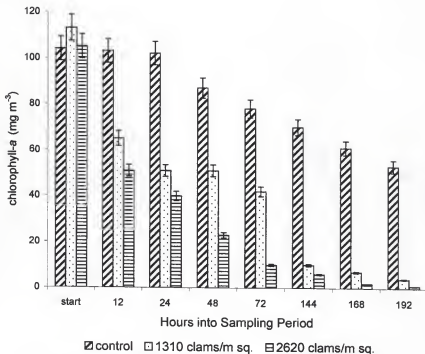


Figure 7. Changes in chlorophyll-a over a 192 hour microcosm experiment. Error bars represent 95% confidence intervals.

clam 1x (from 113 to 65 mg m⁻³) and 51% in the clam 2x (from 105 to 51 mg m⁻³) over this time period.

At the end of eight days, chlorophyll-a in the control microcosms declined 65% (from 104 to 61 mg m⁻³). In the clam microcosms, chlorophyll-a levels declined by an average of 96% in clam 1x (from 113 to 10 mg m⁻³) and 99% in clam 2x microcosms (from 105 to 2 mg m⁻³). Significant differences were seen between the control and the clam 1x ($p=0.049$) and clam 2x ($p=0.015$) microcosms, while no significant difference existed between the clam microcosms ($p=0.702$).

Turbidity (NTU's) was strongly correlated with chlorophyll-a in the control ($r=0.89$), clam 1x ($r=0.97$) and clam 2x ($r=0.98$) microcosms, meaning that the turbid water consisted primarily of phytoplankton and not other suspended particulates (Mann 1988). In both clam microcosms, there was a strong correlation between turbidity and bacterioplankton ($r=0.91$) and chlorophyll-a ($r=0.98$). As all experienced large reductions in the clam microcosms, this suggests that the dense assemblages of filter-feeding *Corbicula* essentially stripped the water column of small particles. It has been suggested by Lauritsen (1986b) and Way et al. (1990) that *Corbicula* are nonselective filter-

feeders, and that these bivalves would remove all particles from the water column that were of acceptable size and possessed weak evasive capabilities.

The significant reductions in turbidity and chlorophyll-a in the clam microcosms support hypotheses that filter-feeding mollusks such as *Corbicula* may control water clarity in many rivers (Gardner et al. 1976, Cohen et al. 1984, Lauritsen 1986b, Phelps 1994) and lakes (Mackie 1992). While increases in water clarity may improve conditions for submerged aquatic vegetation (Phelps 1994), this dramatic reduction of plankton may also be removing the base of the pelagic food chain, thereby negatively affecting heterotrophic organisms by reducing the availability of food. This question is assessed in the remainder of this chapter.

Rotifers

The rotifer assemblages in all microcosms were dominated by *Conochiloides dossauris* and *Trichocera multicrinis* throughout the experiment. All microcosms showed considerable decreases in total rotifer biomass over the course of the experiment, 64% in the control, 73% in clam 1x, and 88% in clam 2x (Figure 8). While rotifer

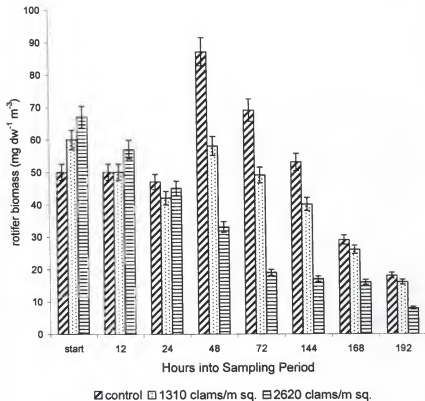


Figure 8. Changes in rotifer biomass over a 192 hour microcosm experiment.
Error bars represent 95% confidence intervals.

biomass decreased by an average of 73% (from 60 to 16 mg $\text{dw}^{-1} \text{m}^{-3}$) in the clam 1x microcosms over the course of the experiment (192 hours), this was not significantly different ($p=0.724$) when compared to the control microcosms.

Similarly, the average rotifer biomass decreased 88% (from 67 to 8 mg $\text{dw}^{-1} \text{m}^{-3}$) in the clam 2x microcosms, and was not significantly different from the control microcosms ($p=0.209$) or clam 1x ($p=0.595$) microcosms.

While not statistically significant, loss of rotifer biomass in the microcosms containing clams (73% and 88%) was greater than that observed in control microcosms (64%).

While grazing by cladocerans and copepods appears to exert the most significant pressure on rotifers, the greater loss of rotifer biomass in the clam microcosms suggests that filter-feeding *Corbicula* do exert some direct grazing pressure on weak-swimming rotifers. This influence is seen in the strong correlation in the clam microcosms between decreases in rotifers, phytoplankton and turbidity ($r=0.82$ and 0.78 in clam 1x and $r=0.94$ and 0.88 in clam 2x), compared with $r=0.46$ and 0.37 in the control microcosms. The decreases were much more significant and much stronger correlated in the clam microcosms compared to the control.

It is likely that the loss of rotifers in the control microcosms (from 50 to 18 $\text{mg dw}^{-1} \text{m}^{-3}$) were brought about by predation from larger macrozooplankton grazers (cladocerans and copepods).

Macrozooplankton

Cladocerans were dominated by *Daphnia ambigua* and *Eubosmina tubicens*. Biomass in all microcosms increased over the course of the experiment. While highly variable, cladoceran biomass in the control microcosms increased from 2 to 22 $\text{mg dw}^{-1} \text{m}^{-3}$, from 5 to 9 $\text{mg dw}^{-1} \text{m}^{-3}$ in the clam 1x, and 3 to 8 $\text{mg dw}^{-1} \text{m}^{-3}$ in the clam 2x over the course of the experiment (Figure 9). Cladoceran biomass in the control was not significantly different from the clam 1x ($p=0.879$) or clam 2x ($p=0.459$) microcosms nor were the clam microcosms significantly different from one another ($p=0.756$).

Biomass for larger planktonic copepods also increased significantly in all three treatments over the course of the experiment (Figure 17). Numerically dominated by *Diaptomus dorsalis*, copepod biomass ($\text{mg dw}^{-1} \text{m}^{-3}$) increased 341% in the control, 338% in clam 1x and 302% in clam 2x microcosms. Copepod biomass in the control was not significantly different from the clam 1x ($p=0.996$) or clam 2x ($p=0.999$)

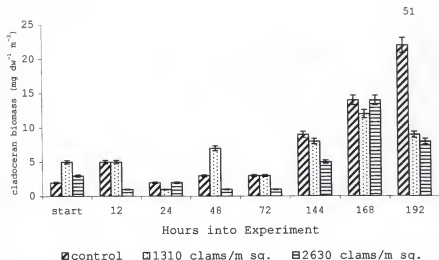


Figure 9. Changes in cladoceran biomass in the microcosm experiment.
Error bars represent 95% confidence intervals.

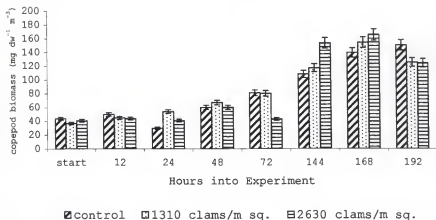


Figure 10. Changes in copepod biomass in the microcosm experiment.
Error bars represent 95% confidence intervals.

microcosms, nor were the clam microcosms significantly different from one another ($p=0.999$). This similarity among the different treatments was not unexpected in this experiment as the macrozooplankton were free of predation from fish.

Copepod assemblages are limited primarily by food limitations and the amount of predatory pressure from planktivorous fish (Anderson et al. 1978, Black and Harrison 1988, Arnotte and Vanni 1993). With the absence of fish predators, it would be likely that macrozooplankton (cladocerans and copepods) biomass may increase if food (rotifers, bacterioplankton, and phytoplankton) were not limiting. Growth rates of cladocerans and increases in copepod biomass through nauplii and copepodite stages vary greatly among species and are directly related to environmental conditions and food availability (Wetzel 1983, He et al. 1994). With sufficient oxygen (the microcosms were aerated), optimal water temperature (24°C) and hypereutrophic water, it was thought that conditions were ideal over the 192 hour period for larger zooplankton to graze on the smaller rotifers and phytoplankton, thereby increasing in biomass.

There was a significant positive correlation between copepod and cladoceran increases in the control ($r=0.92$), clam 1x ($r=0.80$) and clam 2x ($r=0.87$) microcosms. The increase in both calanoid and cyclopoid predaceous copepods and suspension-feeding cladocerans suggests that these groups were grazing primarily on smaller rotifers, bacterioplankton and phytoplankton cells and not on each other, as all groups increased in biomass over the course of the experiment.

There was a strong negative correlation between copepod and rotifer biomass in control ($r=-0.59$), clam 1x ($r=-0.82$) and clam 2x ($r=-0.72$) microcosms, as well as with phytoplankton in the control ($r=-0.97$), clam 1x ($r=-0.82$) and clam 2x ($r=-0.72$) microcosms. Although not as strong, there was a negative correlation between cladoceran and rotifer biomass in the control ($r=-0.77$), clam 1x ($r=-0.53$) and clam 2x ($r=-0.53$) microcosms, as well as with phytoplankton in the control ($r=-0.86$), clam 1x ($r=-0.55$) and clam 2x ($r=-0.42$) microcosms.

This strong correlation (especially with copepods) certainly suggests that macrozooplankton grazing exert a significant negative impact on rotifer, bacterioplankton and

phytoplankton abundance. These results are consistent with experimental studies assessing the impact of zooplankton grazing on smaller-bodied forms (Dawidowicz 1990, Elser et al. 1990).

Conclusions

Conclusion 1. Smaller-sized rotifers, phytoplankton and bacterioplankton decreased in this experiment.

This is likely due to predation by cladocerans and copepods, as well as retention by filter-feeding clams. The overall rate and amount of the decrease varied between treatments (control versus clams). The results from this experiment strongly suggest that filter-feeding and retention by *Corbicula* have the potential to alter planktonic food web structure in hypereutrophic waters.

Conclusion 2. In comparison to the control, there were significant declines in turbidity, bacterioplankton and chlorophyll-*a* levels in the clam microcosms.

This strongly suggests that *Corbicula* are able to filter and retain particles in this size range, directly impacting the base of the food web. Rotifer decline, however, was not significantly different in the clam microcosms relative to the control. This also suggests that *Corbicula* do not exert a more negative affect on particles

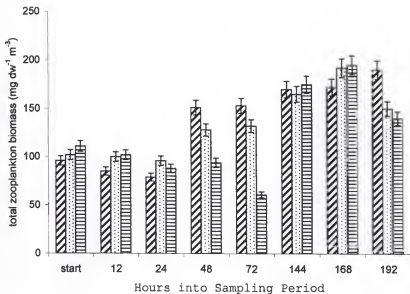
in this size range than does grazing by copepods and cladocerans. While Valiela (1991) hypothesized that the loss of small particles would negatively affect larger macrozooplankton, this was not seen to be the case, at least in this brief experiment.

The larger cladocerans and copepods are out of the particle range preferred by *Corbicula*, and it is unlikely that these organisms would be directly filtered and retained by these clams (Way et al. 1990). Small particles such as suspended solids (turbidity), bacterioplankton and phytoplankton were virtually non-existent in the clam microcosms at the end of this experiment. Because of this significant reduction at the base of the food chain, it is suggested that cladoceran and copepod abundance would have eventually decreased in the clam microcosms if the experiment had continued beyond 192 hours. As *Corbicula* would have eventually eliminated all of the smaller food particles (bacterioplankton, phytoplankton, and rotifers), food for macrozooplankton may have become limiting. This experiment demonstrated that *Corbicula* can alter levels of rotifer communities that are able to feed on phytoplankton cells, reducing this energy transfer up the food chain.

Conclusion 3. *Corbicula* were not able to change overall zooplankton biomass (Figure 11), as there was no significant difference in the control when compared to the clam 1x ($p=0.982$) and clam 2x ($p=0.728$) microcosms.

Changes in plankton communities are directly and indirectly altered by the presence of *Corbicula*. The direct impacts to smaller particles in the water column such as phytoplankton is clear and significant (Figure 7). Even with a doubling of clam density, there was no significant difference between the clam 1x and clam 2x microcosms ($p=0.832$). This further confirms that large filter-feeding mollusks such as *Corbicula* and *Dreissena* do not appear to be able to successfully prey on larger, motile zooplankton such as cladocerans and copepods (Silverman et al. 1995).

It is important, however, to assess *Corbicula*'s secondary impacts on larger organisms such as cladocerans, copepods and larval fish carefully. If *Corbicula* virtually eliminates smaller-bodied particles from the water column (essentially removes the base of the food chain), it is logical to conclude that the secondary impacts on larger organisms may be equally dramatic and significant (Carpenter et al. 1985). If you eliminate or significantly change the base of the food web, one would expect that the higher



▨ control ▤ 1310 clams/m sq. ▧ 2630 clams/m sq.

Figure 11. Changes in total zooplankton biomass over a 192 hour microcosm experiment. Error bars represent 95% confidence intervals.

trophic forms may be affected as well (Colinvaux 1986). The purpose of the next experiment was to explore this idea in more detail.

CHAPTER 4
SURVIVAL OF LARVAL FISH IN LABORATORY MICROCOSMS
IN THE PRESENCE OF Corbicula fluminea

Introduction

It was clearly demonstrated in the previous chapter that *Corbicula* possesses the capability, through its filter-feeding behavior, to significantly reduce turbidity (with attached bacterioplankton), phytoplankton, and rotifers. Freed from predation, large zooplankton (cladocerans and copepods) are important grazers on these small-bodied plankton, as strong negative correlations were seen between increases in cladoceran and copepod biomass and decreases in turbidity, bacterioplankton, phytoplankton and rotifers.

Knowledge of how larval fish grow and survive and the importance of prey availability are critical to understanding recruitment processes (Welker et al. 1994). Adequate densities of plankton are an important and essential source of food for the larvae of most fish species (Black and Harrison 1988). The kinds or types of ingested food particles change rapidly with the growth of larval fish. The mean size of prey items consumed often increases

as the fish grow from early to late larval stages (Welker et al. 1994). As larvae begin to grow, their dietary requirements shift from small-bodied organisms such as bacterioplankton and protozoans to larger organisms such as phytoplankton and rotifers (Figure 12) (Byers and Vinyard 1990).

A great deal of literature exists on the swimming behavior, vertical migration and feeding of larval fish on plankton (Black and Harrison 1988, Gee 1991). Larval fish generally are either suspension feeders or particulate feeders (Edmondson 1959). Suspension-feeding fishes retain phytoplankton and zooplankton by filtering large volumes of water (Sanderson and Wassersug 1990), engulfing several prey items simultaneously, and are relatively nonselective in retention of these items (Sanderson and Cech 1992). These fish filter and retain planktonic particles in a way similar to that of *Corbicula*. As with nonselective filter-feeding clams (Jorgensen 1966, Lauritsen 1986), suspension-feeding fishes can profoundly modify overall plankton abundance and community structure (Drenner et al. 1987, Hanazato and Yasuno 1989).

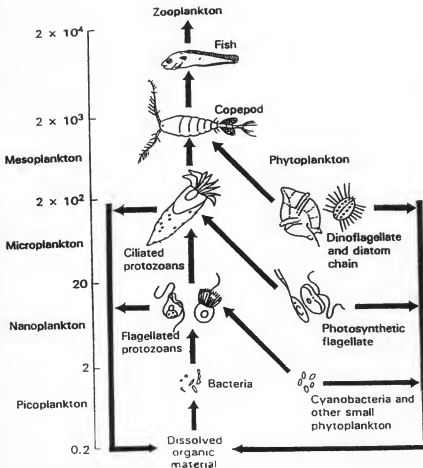


Figure 12. General size structure of a marine planktonic food web (from Fenchel 1974).

Particulate feeders visually orient to and attack individual zooplankters (Sanderson and Cech 1992). The feeding strategy for any particulate feeder is to take in the highest quality and quantity of food with the least effort (energy expenditure). Food selectivity usually is based on particle size and shape (Drenner et al. 1984). In order to avoid starvation, it is important for metalarvae (post-yolk-sac larvae) to find an abundance of nonmotile prey organisms or to be able to catch, handle, and ingest large prey items without expending considerable amounts of energy.

The embryonic period in a developing individual is characterized by complete dependence on the attached yolk sac for life-sustaining nutrition. An extremely critical period in the life of a fish is the transformation from the embryonic to the larval phase. The beginning of the larval period is signified by the ability of the fish to capture food organisms (Balon 1975). The critical factor for the survival of the larvae is the availability of food of the proper size, abundance, and nutritional value during the first few days of feeding (Lasker 1978, McElman and Balon 1979). When the nutritional yolk sac has been completely

absorbed, the larval fish must now actively seek, select, capture, and ingest prey organisms or risk death due to starvation. This means that small protozoans, diatoms, dinoflagellates and rotifers must be available in sufficiently high densities if the larvae are going to be able to capture enough food to avoid starvation. Also, as the larval fish grows, a larger size range of prey becomes available (Braum 1978), and their risk of being consumed by filter-feeders diminishes.

As documented in Chapter 3, laboratory microcosms that contained the filter-feeding *Corbicula* experienced significant losses of turbidity, phytoplankton, bacterioplankton and rotifers. It is the purpose of this experiment to assess the direct (filtering and retaining fish eggs) and indirect impacts (competition for small-bodied organisms) between the filter-feeding clam (*Corbicula*) and a particulate feeding larval fish.

Will we see significant differences in survival of fish larvae in control versus clam-containing microcosms (H_0) or is it possible that *Corbicula* will suppress small-bodied organisms in the clam-containing microcosms, causing increased mortality among metalarval fish due to

insufficient food being available (H_A)? Will sufficient small-bodied organisms (bacteria, rotifers, phytoplankton) be available in sufficient abundance to ensure the survival of fish that have matured from the embryonic period to the metalarval (post-yolk-sac larvae) life phase? These questions were addressed in this chapter.

Methods

Corbicula from Hogtown Creek in Gainesville were collected by a Ponar grab. To minimize stress to the animals, approximately 4.0 liters of highly oxygenated, stream water along with sandy coarse substrate that the infaunal organisms inhabited were transported to the University of Florida (UF) campus 2.0 kilometers away. In a constant environmental chamber in UF's Black Hall, substrate, clams and stream water were placed in an aerated 113-liter aquarium. Inside the environmental chamber, automatic timers produced 12 hours of light and 12 hours of dark to simulate natural conditions found in early September in this area. Water was set at 22°C, the temperature of the stream. The clams were held under these conditions for the next 48 hours in order to acclimate, reduce stress and to be consistent with the previous experiment.

After 48 hours, nine microcosms were set up in the environmental chamber. Each microcosm had 2.5 cm of clean rinsed builder's sand and 4.0 liters of hypereutrophic (chlorophyll-a concentrations between 90 and 100 mg m⁻³) water collected from a nearby lake was added. The collected water was supersaturated (oxygen concentrations >200% saturation), dark green in color and presumably contained an abundant and diverse assemblage of planktonic organisms. All microcosms were gently aerated with an airstone to reduce settling by plankton and fish eggs.

Four hundred and fifty fertilized "eyed" fathead minnow, *Pimephales promelas*, eggs were placed in a porcelain tray. Under a magnifying glass, 50 of the fertilized adhesive eggs were carefully removed from the tray and added to each microcosm. Three microcosms contained only lake water (the controls), and six microcosms each contained 50 fertilized fish eggs. A portion (3 clam-containing microcosms) of the experiment was terminated after 336 hours (14 days) and the remaining portion (3 clam-containing microcosms) after 504 hours (21 days). This time period was chosen because it was hypothesized that fish eggs would take approximately 7 days to hatch, the larvae absorb the

nutritional yolk sac in another 7 days (total of 14 days) and actively begin to seek food (plankton) once the yolk sac was absorbed. The 3 control microcosms were used for the entire 504 hour (21 day) period.

Turbidity (NTUs), chlorophyll-a (mg m^{-3}) and rotifer biomass ($\text{mg dw}^{-1} \text{m}^{-3}$) were measured weekly (0, 168, 336, and 504 hours). As phytoplankton and microzooplankton (rotifers) are the dominant food source of many larval fish (Papoulias and Minckley 1992), it is extremely important to assess changes in their abundance over this time period. In particular, chlorophytes and rotifers are an important food source for larval *P. promelas* (Shaw et al. 1995). The weekly sampling interval was chosen as it was hypothesized from the results of the previous chapter that levels of small particles might be virtually nonexistent after the first 7-day period (168 hours). Therefore, daily measurements were not warranted and would not yield significant information. Each microcosm was visually inspected daily, and the condition of the eggs/larvae noted. The surviving (evident by viable appearance with yolk sac attached or by swimming) number of larvae was recorded each day.

Results and Discussion

Suspended Particles

At the start of the experiment, turbidity averaged approximately 12 NTU's and chlorophyll-a ranged between 93 and 100 mg m⁻³, both indicative of hypereutrophic water. Turbidity (Figure 13) and chlorophyll-a (Figure 14) were dramatically reduced in all 6 clam and 3 control microcosms. Turbidity and phytoplankton (chlorophyll-a) were barely detectable after 7 days (168 hours) and remained so for the remainder of the experiment (336 hours to 504 hours). There were no significant differences in turbidity in the control compared to the clam 1x ($p=0.369$) and clam 2x ($p=0.219$) microcosms, nor were the clam microcosms significantly different from one another ($p=0.326$). Once again, this suggests that settling and macrozooplankton grazing reduce suspended solids and small-bodied organisms, as turbidity in the control was reduced by 43%. With clam microcosms experiencing 91% and 93% reductions, it is clear that filtering and retention by *Corbicula* exert an additional influence on suspended solids and small-bodied organisms.

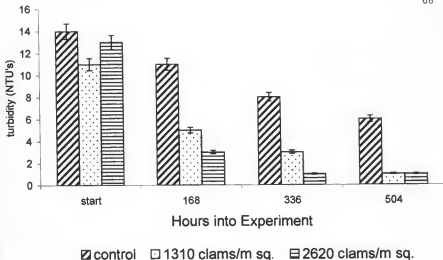


Figure 13. Changes in turbidity over a 504 hour (21 day) microcosm experiment. Error bars represent 95% confidence intervals.



Figure 14. Changes in chlorophyll-a over a 504 hour (21 day) microcosm experiment. Error bars represent 95% confidence intervals.

Rotifer biomass experienced an 81% reduction in the control, 80% in clam 1x and 85% in clam 2x microcosms (Figure 15). The rotifer reduction experienced in the control was insignificant compared to the clam 1x ($p=0.369$) and clam 2x ($p=0.219$) microcosms. This suggests that grazing by cladocerans and copepods, and not *Corbicula*, had an important direct role in preying on and retaining the organisms in this size range. These results reconfirm that *Corbicula* seem to be able to reduce small particles (rotifer size and smaller) directly but have little additional effect on planktonic organisms larger than rotifers.

Shifts in zooplankton community structure may be caused by the loss of phytoplankton to filter-feeding mollusks. With less food available, sensitive zooplankton species may be replaced by others less vulnerable to fish predation (Lynch 1979). This has been witnessed in the St. Lawrence River and Great Lakes, where filter-feeding *Dreissena* has become the dominant mollusk, and has given rise to *Bythotrephes*, the dominant crustacean zooplankter. Overall zooplankton biomass in many areas of the Great Lakes has not been reduced from its historic average, although community structure may have dramatically changed (He 1994).

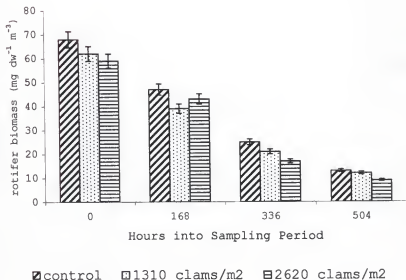


Figure 15. Change in rotifer biomass over a 504 hour (21 day) microcosm experiment. Error bars represent 95% confidence intervals. Clam densities are in m^2 .

Ecologists predict that this exotic species may reduce recruitment of some Great Lakes fish (MacIssac et al. 1991).

Larval Fish

It has been shown in numerous studies (Papoulias and Minckley 1992) that the problem of recruitment failure in many fish species is a result of inadequate zooplankton standing crops (Post and McQueen 1987). If metalarval fish must rely on small-bodied organisms in order to survive, it was hypothesized that reductions in turbidity (with accompanying phytoplankton, bacterioplankton, and nanoplankton) and rotifers would lead to increased mortality due to starvation. The "critical period" when fertilized fish eggs (eyed egg) matured from the embryonic membrane to the free endogenous (yolk sac attached) stage was approximately 7 days. The yolk sacs of all fish seemed to be absorbed completely (non-visual) by the end of the 8th day. After the 8th day (192 hours) of the experiment, it appeared that *P. promelas* was forced to switch from endogenous (yolk) to exogenous (zooplankton) forms of nutrition.

These metalarvae were now living in water with only 7%-9% of the original suspended solid concentration in the clam

microcosms and 15%-20% of the original rotifer biomass. The microcosm experiment reported in Chapter 3 demonstrated a 300% or more increase in copepod biomass in all microcosms (with the assumption that similar results occurred here). With the dramatic reduction in food (phytoplankton and rotifers), large increases in cladoceran and copepod biomass likely occurred as a result in growth of the various life stages (nauplii to copepodite to adult) of zooplankton present. This was seen by Lynch (1979) as well, where there was a strong negative correlation between rotifer and phytoplankton biomass and calanoid copepod biomass.

The planktonic composition in the microcosms consisted primarily of large-bodied cladocerans and copepods at this time. Could the apparent shift from small-bodied phytoplankton and rotifers to larger-bodied cladocerans and copepods negatively affect the feeding of metalarvae (H_A)? At this stage in their life history, larval fish are approximately the same size (12 mm - 15 mm) as a calanoid copepod (Houde 1978). Generally speaking, larval movement appeared to be a gliding motion through the water column. This is consistent with the feeding behavior of larval fish as reported by Moyle and Cech (1982). In contrast, motile

raptorial-feeding calanoid copepods such as *Diaptomus* and *Calanus* usually move in a much more jerky swimming behavior (Lynch 1979). Because of the differences in swimming behavior of the prey (jerky movement) versus the predator (gliding movement), it was thought that it would be extremely difficult for the larvae to catch and ingest these large zooplankters.

The successful transformation from embryo to larvae averaged 94% in the control tanks (141/150) and 90% (135/150) and 91% (137/150) in the two sets of clam microcosms (Figure 16). At the end of 14 days (336 hours), the numbers of larvae in 3 control and 3 of the clam (clam 1x) microcosms were carefully enumerated with the aid of a dissecting microscope. The water from each was poured into a 37-liter microcosm. All swimming larvae from each microcosm were individually counted. If there were fewer than 50 (the original total in each microcosm) unhatched fish eggs, the water column was assessed and the sand was carefully examined under a dissecting microscope to account for this loss. Extreme care was taken to minimize any handling impacts to the larvae. When the egg counts were recorded, the controls were immediately returned to the

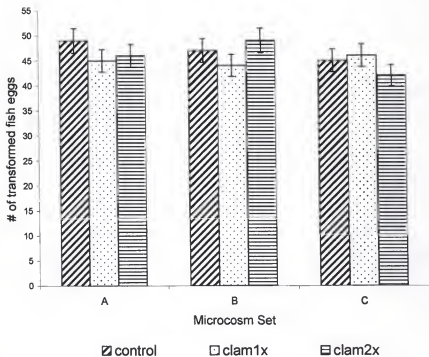


Figura 16. The average number of fish eggs transformed from embryo to larvae after 168 hours (7 days) in microcosms. Error bars raprasant 95% confidence intervals. Clam 1x = 1310 clams/m² and clam 2x = 2620 clams/m².

laboratory chamber where the experiment continued for another 168 hours (7 days). This was done to contrast the control to the clam mesocosms (clam 2x) after 504 hours (21 days) and to compare these results with the results seen after 336 hours (14 days).

The mortality of larval fish in the clam microcosms was much greater than in the controls (Figure 17). The average number of larvae surviving (as indicated by swimming) in the control after 336 hours (14 days) was 39 (78%), whereas, this survival dropped to 12 (24%) in the clam 1x and 9 (18%) in the clam 2x microcosms. After 504 hours (21 days), the survival of larval fish dropped even further, averaging 33 larvae or just 66% of the number the experiment started with in the control compared with 8 (16%) in the clam 1x and 9 (18%) in the clam 2x microcosms (Figure 18).

Based on the results of the previous laboratory microcosm experiment (Chapter 3), it was assumed that the water column in the clam microcosms consisted primarily of large-bodied cladocerans and copepods. If this were the case, it was hypothesized that fish larvae could suffer significant mortality due to food deprivation. Although the stomachs of the larvae were never examined, the drastically

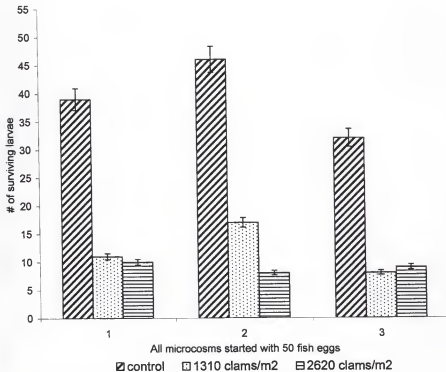


Figure 17. The number of surviving larvae in all microcosms after 336 hours (14 days). Error bars represent 95% confidence intervals. Clam densities in m^2 .

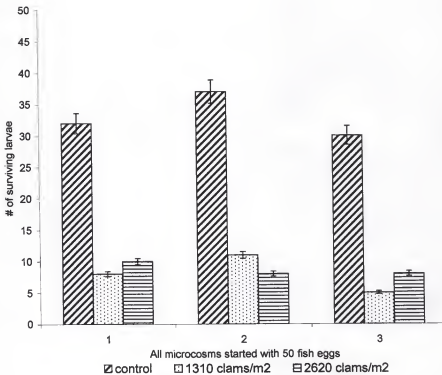


Figure 18. The number of surviving larvae in all microcosms after 504 hours (21 days). Error bars represent 95% confidence intervals. Clam densities in m^2 .

reduced levels of turbidity, phytoplankton and rotifers in the clam microcosms strongly suggest that an inadequate supply of food was available to the exogenous larvae. There was a very strong correlation between larval fish mortality and reductions of turbidity ($r=0.95$), phytoplankton ($r=0.95$) and rotifers ($r=0.96$) in all microcosms.

As has been found in previous laboratory microcosm (Papoulias and Minckley 1990) and pond experiments (Papoulias and Minckley 1992), failure of fish recruitment may be attributed to nutritional deficiency. Marsh and Langhorst (1988) found similar larval mortality in relation to zooplankton densities in a number of southwestern lakes and reservoirs.

Conclusions

Clearly, increased reductions in turbidity, phytoplankton and rotifer biomass in the clam microcosms suggest that the filter-feeding *Corbicula* were able to reduce small-bodied organisms to levels that may have been detrimental to larval fish seeking these food organisms for survival. Now that the metalarval fish had to rely totally on exogenous sources of food items (phytoplankton, rotifers, nanoplankton) that no longer existed at sustainable levels,

increased mortality to fish larvae in all clam microcosms occurred. Therefore, H_0 for this experiment was rejected as there were significant differences in larval fish mortality after 14-21 days in the control versus clam-containing microcosms.

Similar freshwater and marine experiments have examined the feeding behavior, stomach content, dietary requirements, and starvation potential of fish larvae (May 1974, Gadomski and Petersen 1988). Most of these experiments have investigated changes in zooplankton densities as a function of either reduced loading to a water body (Arnotte and Vanni 1993) or grazing by planktivorous fish (Cramer and Marzolf 1970, O'Brien 1979, Drenner et al. 1987). This experiment assessed the ability of *Corbicula* to filter and retain small-bodied organisms (suspended particles, phytoplankton and rotifers), making these organisms unavailable to fish larvae as food, thereby possibly contributing to their mortality from starvation.

CHAPTER 5
QUALITATIVE ASSESSMENT OF THE ALGAL CELL ACTIVITY
ENCASED IN PSEUDOFECES OF Corbicula fluminea

Introduction

The majority of bivalves are thought to derive most of their nutrition from filter-feeding on phytoplankton cells and organic detritus (Barnes 1974). *Corbicula* filter large volumes of water (McMahon 1982, Cole et al. 1992) and are able to remove significant amounts of organic detritus and phytoplankton from the water column (Lauritsen 1986a, Alpine 1992). Growth studies of the Asiatic clam have concluded that most particles removed from the water column are not readily assimilated by the mollusk (Foe and Knight 1986). It is apparent from these studies that the exotic clam releases significant amounts of nutrients back into the water column (Hill and Knight 1981, Lauritsen and Mozley 1989).

Corbicula also are able to bind large amounts of bacteria-laden detritus, phytoplankton, and small rotifers in a protein mucilaginous sheath (Lauritsen 1986b). Partially digested mucous-bound clumps of phytoplankton cells and detrital particles (pseudofeces) are removed from

the water column and sink to the bottom of lakes (Officer et al. 1982, Lauritsen 1986b). It is unclear whether these partially digested bound particles are too large for smaller organisms in the pelagic food chain to be consumed or are large enough to be consumed by larger organisms higher in the food chain. Ross (1994) expressed concern that much of the planktonic energy in the Great Lakes may be becoming benthic because of the binding of planktonic particles by the zebra mussel (*Dreissena polymorpha*). Similarly, the Chinese clam, *Potamocorbula*, has generated large amounts of pseudofeces in San Francisco Bay, increasing energy available to the benthos (Alpine and Cloern 1992).

The eventual fate of the mucous-bound detritus and phytoplankton is very important to nutrient cycling, benthic organisms, and the pelagic food web. Are organisms encased in the mucilaginous sheath alive (actively respiring) and, if so, for how long? Are pseudofeces suspended by convective or wind energy into the water column an important nutrient source? Can *Corbicula* change energy dynamics by concentrating large amounts of food (encasing small cells), thereby making them more available to higher trophic levels?

Most research to date has focused primarily on the fate of fecal pellets released into the water column by pelagic organisms such as fish and zooplankton and deposited onto the sediments by benthic organisms (Nichols and Thompson 1985, Mann 1988). While feces are an important nutrient source for primary production, digested food particles are considered relatively devoid of energy value (Dame et al. 1980, Dame and Dankers 1988). Bound undigested food, however, may represent an important food source to both benthic and pelagic organisms.

It was the purpose of this study to (a) determine if the mucous-bound phytoplankton are active by staining cells and using a direct microscopic technique; (b) if found to be active, determine how long (hours to days) these food cells remain active; and (c) discuss the possible ecological ramifications of *Corbicula*'s ability to remove and bind large amounts of phytoplankton.

Methods

A pure culture of the cyanophyte *Microcoleus* was obtained from Dr. Ed Philips of the University of Florida for this experiment. Fifty milliliters of *Microcoleus* culture was poured into each of thirty 400-mL Kimax beakers, each

containing clean quartz sand and one *Corbicula*. Within one hour, *Corbicula* had seemingly filtered all of the water contained in the beaker and had produced large amounts of pseudofeces. These "green packets" were easily recognizable as greenish clumps collecting on the white sand at the bottom of each beaker. These green packets were removed from each beaker using a large pipette, and transferred to a series of beakers containing filtered lake water.

Activity of the pseudofeces packets in each beaker was determined daily over a thirty-day period. Activity (metabolism and respiration) of the cells was determined by using a bright-field microscopic technique developed by Zimmermann et al. (1978) and described by Bitton and Koopman (1982) and Dutton et al. (1983). To determine the respiratory activity of bacteria (including cyanophytic algae), cells were stained with 0.2% 2-(*p*-iodophenyl)-3-(*p*-nitrophenyl)-5-phenyl tetrazolium chloride (INT). INT reduction by bacteria produces INT-formazan crystals by electron transport system activity (Zimmermann et al. 1978). The active electron transport system is almost a universally accepted component of determining respiring organisms (Zimmermann et al. 1978, Atlas and Bartha 1981). Because

INT acts as an electron acceptor, actively respiring bacterial cells accumulate water-insoluble red INT-formazan crystals that are clearly visible under bright-field microscopy (Bitton and Koopman 1982).

Non-active (dead) algal cells representing control treatments were made by exposing some of the *Microcoleus* culture to short-wavelength germicidal ultraviolet (UV) radiation at a distance of approximately 15 cm for 30 minutes. Algal cells were also killed by exposing them to formaldehyde, glutaraldehyde, and heat (40 minutes at 70°C) and placing them in the dark for twenty-four hours.

At the end of the twenty-four hour period, 0.5 mL of INT was added to each 5 mL sample, and the mixture was incubated in the dark at room temperature for 30 minutes. The sample was then centrifuged at 1,000G_s for approximately 5 minutes. Four milliliters of the sample was decanted, and the remaining 1 ml of pseudofeces was prepared for examination of activity. One drop of the pseudofeces sheath was placed on a glass slide, spread, and fixed by rapidly placing the glass slide over a Bunsen flame (Atlas and Bartha 1981). The slide was covered with a clean glass cover slip. Immersion oil was placed on the prepared slide

to improve the numerical aperture, and the slide was examined with the aid of phase contrast microscopy and illumination at 1000x magnification. This procedure was undertaken to see how a non-active algal cell appears under microscopy and to later compare this image to known active (live) cells.

The phase contrast microscope is useful for visualizing living microorganisms and eliminates the necessity of staining to view certain microbial structures. It is designed to separate direct background light from the light passing through the unstained microorganism. It was decided that this microscopic method would be acceptable as INT-formazan crystals could be easily observed within the cyanophyte cell wall.

With the exception of cyanophytes, all algae are eukaryotic, having cells delineated by a cytoplasmic membrane and containing a nucleus, storage vacuoles, Golgi apparatus, mitochondria, endoplasmic reticulum, and ribosomes in the cytoplasm. Such complex internal structures may hinder identification of INT-formazan crystals within the cell membrane. Preliminary laboratory investigations using the chlorophytes *Chlorella vulgaris* and

Scenedesmus bijuga confirmed this, as microscopic differentiation between red oval INT-formazan crystals and internal organelles such as vacuoles proved to be extremely difficult, if not impossible. Because of this difficulty, it was decided that chlorophytes would not be used in the activity experiments. Because prokaryotic cells lack large internal membranous structures, it was thought that cyanophytes would be prove excellent for determining the activity of algal cells using the INT-formazan technique.

Results and Discussion

Algal cells subjected to formaldehyde, glutaraldehyde, UV radiation, and heat were examined under the phase contrast microscope for activity. These cells contained no red formazan crystals (Figure 19) and were considered to be non-active (dead). Using what was considered active (live) algal cells, several cells of *Microcoleus* were examined under the phase contrast microscope for activity. These cells clearly contained bright red INT-formazan crystals (Figure 20) within their cell walls and were considered to be active. Figures 19 and 20 certainly suggests that the INT-formazan technique originally proposed by Zimmermann et al. (1978) can successfully be used to differentiate between



Figure 19. Under phase contrast microscopy, no internal structures or large INT-formazin crystals are evident in a non-viable *Microcoleus* cell (photo courtesy of the University of Florida, Dept. of Fisheries and Aquatic Sciences).

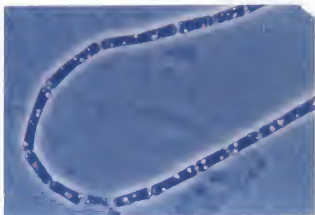


Figure 20. Viable (respiring) *Microcoleus* cells clearly contain bright INT-formazin crystals as seen at 1000x magnification (photo courtesy of the University of Florida, Dept. of Fisheries and Aquatic Sciences).

live and dead cyanophyte cells (objective #1 of this experiment).

Activity of algal cells encased in the pseudofeces produced by *Corbicula* was noted daily, and cells were still active (presence of formazan crystals) up to eighteen days from the start of the experiment. After eighteen days, the breakdown of the pseudofeces and the brown color of algal cells made determination of activity extremely difficult. Between 18-22 days, it was very difficult (if not impossible) to distinguish colors and hence activity. After twenty-two days, algal cells appeared dark brown (possibly indicating attachment of bacteria on cell wall) and were therefore deemed to be non-active (objective #2 of this experiment).

Many different variables (light, nutrient availability, presence of grazers) control the rate of growth, reproduction and survival of algal cells (Valiela 1991). There is also a species specificity of algal cell longevity (Lauritsen 1986a), ranging from several days to weeks (Stockner 1988, Valiela 1991). Because of this large variability, it is difficult to interpret the overall consequences to phytoplankton populations of cells that pass

through *Corbicula* but are not assimilated by the mollusk. One thing is for certain, *Corbicula* are non-selective algal filter-feeders (McMahon 1983, Foe and Knight 1985), filter large volumes of water and produce significant amounts of pseudofeces from algae not totally assimilated (Lauritsen and Mozley 1989).

Generally speaking, phytoplankton populations are protected by their small size, large numbers and rapid growth rate (Valiela 1991). Therefore, it is very difficult for herbivores to affect local phytoplankton populations significantly because algal cells are so small, numerous and widely distributed (Levin and Segel 1976, Lynch 1979, Valiela 1991). With *Corbicula*'s ability to package these small cells, pseudofeces may now be large enough to be consumed by many different organisms. The ecological consequence of this may range from increased water clarity (*Corbicula* "graze" more algal cells than zooplankton) to concentrating algal cells and making them available as food for larger organisms, where they would normally not have been available if they weren't packaged in pseudofeces. Active cells encased in pseudofeces represent available energy (Bird and Kalff 1986, Asmus and Asmus 1991) to

organisms in a concentrated form and may prove beneficial to both benthic as well as phytophagous fish (Drenner et al. 1984, Flamarique-Novales 1993).

The H_0 was rejected for this experiment as the presence of *Corbicula* clearly correlated with an increase in the amount of pseudofeces being deposited on the benthos. This preliminary experiment assessing the temporal activity of cyanophytes encased within the semi-impermeable membrane of the pseudofeces may be extremely important in determining if water transparency changes are temporary. If algal cells removed from the water column are temporarily encased in pseudofeces (increasing water transparency), active cells previously encased in pseudofeces and resuspended back into the water column days may later decrease water transparency. This temporary change in water clarity could disrupt light intensity (from clear back to turbid) and change nutrient concentrations (from low to high algal cell abundance) throughout the water column.

CHAPTER 6
ASSESSING THE IMPACT OF Corbicula fluminea
AND Oreochromis aureus ON WATER QUALITY AND
PLANKTON IN OUTDOOR MESOCOSMS

Introduction

The deliberate control of physical, chemical, and biological variables allows the experimenter to gain important inferences from laboratory results to be further refined and tested in the field (Colinvaux 1986, Hairston 1989). The principal goal of the microcosm experiments presented in previous chapters was to take observations seen under controlled conditions and to generate hypotheses that could be tested under more natural conditions. The microcosm experiments clearly fulfilled that goal.

The purpose of this study was to mimic more natural conditions by using outdoor mesocosms. The H_0 was that there would be no significant physical or biological differences in any of the mesocosms containing clams (*Corbicula*), fish (*Oreochromis*), or a combination of both clams and fish. It was hypothesized that the filter-feeding *Corbicula* and omnivorous planktivore *Oreochromis* would react physiologically differently to seasonal changes in water

temperature, from a winter low of 7° C to a summer high of 33° C. Because of differing feeding rates under these water temperatures, substantial differences in dissolved oxygen (DO) levels as well as phytoplankton and zooplankton biomass may be seen in the different treatments at different times of the year. Water temperatures at which *Corbicula* and *Oreochromis* are optimally feeding are different. Because of this, it was possible that phytoplankton and rotifer communities may be suppressed during maximum *Corbicula* and *Oreochromis* grazing periods, but increase during stressful periods (extreme cold or hot) when feeding may be inhibited (H_A).

Three experiments were conducted between 18 November - 21 December 1992, 29 March - 23 April 1993, and 11 September - 11 October, 1993. These time periods were chosen as they provided a wide range of temperature and light conditions and represented both optimal as well as stressed physiological conditions for both *C. fluminea* (McMahon 1983) and *O. aureus* (Shafland and Pestrak 1982).

Methods

Twelve circular fiberglass mesocosms measuring 2.4 m (radius) x 0.9 m (deep) were set up on a levee directly

adjacent to an experimental pond at the U.S. Geological Survey's (BRD) Florida/Caribbean Science Center in Gainesville. Five centimeters of clean builder's sand was added to each mesocosm to mimic the substrate seen in nearby rivers and streams. One thousand, four-hundred and twenty liters of pondwater from the adjacent hypereutrophic (a visual assessment of dark green water) pond was pumped into each mesocosm until the water level was 1.3 m. Three mesocosms containing only water acted as experimental controls (herein referred to as "control"). Three mesocosms contained *Corbicula* (total wet weight = 1848 grams, around 800 individuals), herein referred to as "clams". Three contained both *Corbicula* (total wet weight = 1848 grams) and the facultative omnivorous cichlid *Oreochromis*, (total wet weight = 6 kg, 3- 4 individuals), herein referred to as "clam+fish". Three contained only *Oreochromis* (total weight = 6 kg), herein referred to as "fish".

Samples were taken from each mesocosm at noon daily for the first 10 days of the experiment (10 samples) and approximately every other day for the next 20 days (10 samples). Water temperature ($^{\circ}\text{C}$) and dissolved oxygen (mg/L^{-1}) at both the bottom and top of the water column were

recorded in each mesocosm with a Hach meter. Similarly, pH was taken with the use of an Orion pH meter. A one-liter water sample was collected by a Niskin bottle from both the top and bottom of each mesocosm and combined to represent an integrated sample. Water samples were analyzed intermittently (either daily during the first half of the experiment to every other day during the last half) for phytoplankton (expressed as chlorophyll-a), rotifers, and macrozooplankton (cladocerans and copepods) biomass.

Rationale for Statistical Methods

The purpose of this study was to examine **if** statistically significant changes occur, either physico-chemical or biological, over the duration of seasonal experiments (both intra- and intermesocosm). As the sample size is considered "small" ($n < 30$) for each experiment, the paired t-test and F-test ($p < 0.05$) obtained from a one-way ANOVA were considered the most appropriate methods (Mendenhall 1987). If physico-chemical and/or biological statistically significant differences developed in the mesocosms, **when** these differences developed is also an important question that was addressed in this experiment. This can be seen on all of the graphs when the error bars

representing 95% confidence intervals on bar graphs do not overlap.

Why significant differences occurred was an extremely important question addressed in this chapter. Basic ecological principles, results from other experiments found in the literature, and statistical tests such as the significance of association of the various variables (bivariate correlations) and strength of linearity (multiple linear regression models) with variables compared against each other were undertaken with the aid of the computer statistical package SPSS.

Results and Discussion

Water Temperature

Water temperatures ranged between 7°C and 23°C during the winter (November/December) experiment (Figure 21). No significant differences ($p > 0.05$) for the mean, maximum, and minimum water temperatures as well as their variability were noted in any of the mesocosms. This was extremely important as water temperatures must be similar among the mesocosms in order to assess the feeding behavior of *Corbicula* and *Oreochromis* under identical thermal conditions.

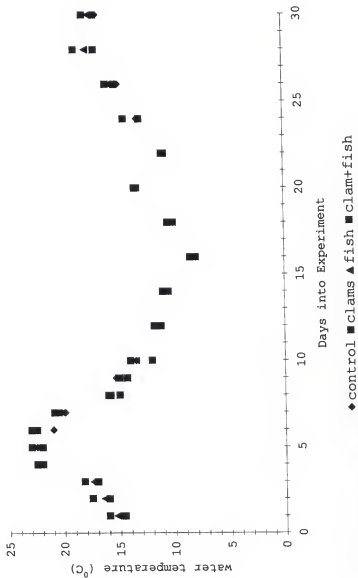


Figure 21. Changes in mesocosm water temperature during the winter experiment.

Water temperatures ranged between 17°C and 29°C during the spring (March/April) experiment (Figure 22). No significant differences ($p>0.05$) for the mean, maximum, and minimum water temperatures were noted in any of the mesocosms.

Water temperatures ranged between 25°C and 32°C during the summer (September/October) experiment (Figure 23). No significant differences ($p>0.05$) for the mean, maximum, and minimum water temperatures, as well as their variability, were noted in any of the mesocosms. There was never any difference between water temperatures just below the surface and just above the bottom of the mesocosm at any time of the year, indicating that the 1 m water column was well mixed with no apparent stratification ever occurring.

Lauritsen and Mozley (1989) found that filtration and excretion rates of *Corbicula* were positively correlated with water temperature. Garnier and Mourelatos (1991) clearly demonstrated seasonal periodicity of phytoplankton losses in a well mixed shallow French lake from zooplankton grazing as losses far exceeded primary production in summer but not in winter. Shafland and Pestrak (1982) and Lazzaro (1987) observed feeding rates of *Oreochromis* over a wide range of

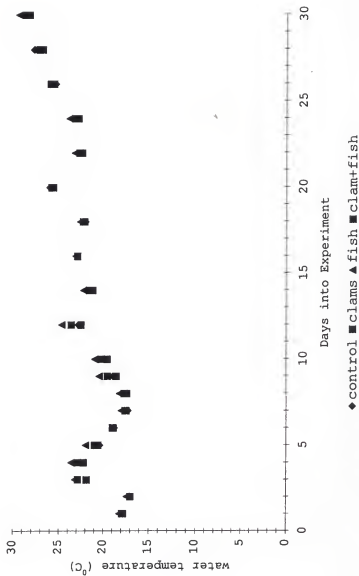


Figure 22. Changes in mesocosm water temperature during the spring experiment.

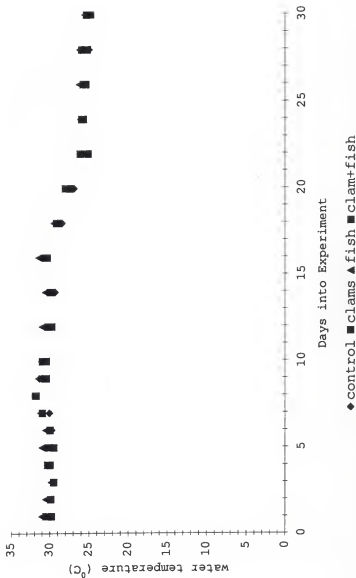


Figure 23. Changes in mesocosm water temperature during the summer experiment.

water temperatures and concluded that this process changes in response to water temperature. With these studies in mind, it seemed logical to expect both the physico-chemical and biological changes observed in the mesocosms would strongly exhibit seasonal periodicity as well, as the feeding rates of *Corbicula* and *Oreochromis* are different from one another at different times of the year.

Dissolved Oxygen

Dissolved oxygen (D.O.) ranged from a minimum of 8.7 mg L⁻¹ to a maximum of 14.6 mg L⁻¹ over the course of the winter sampling (Figure 24). At these water temperatures, D.O. levels were usually supersaturated, ensuring that sufficient DO existed for both clams (Belonged 1991) and fish (Ale 1987). There was high variability in mesocosms containing fish when compared to the non-fish mesocosms (control, clams). Although highly variable, various multiple comparison tests (Tukey, Scheme, Bonferroni, LSD, Dunnett C, Waller-Duncan) all indicated that these differences were not significant during the course of the experiment.

Dissolved oxygen (D.O.) ranged from a minimum of 10.2 mg L⁻¹ in the fish enclosures to a maximum of 19.9 mg L⁻¹ in the control mesocosms during the spring experiment (Figure

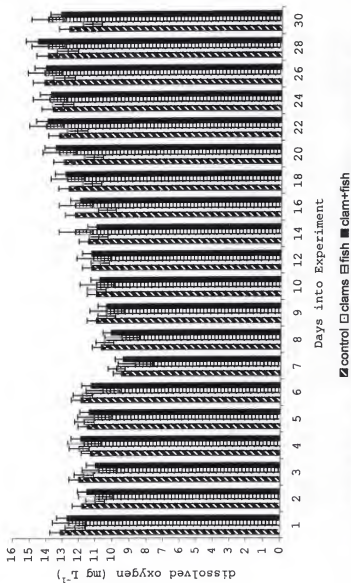


Figure 24. Changes in mesocosm dissolved oxygen during the winter experiment. Error bars represent 95% confidence intervals.

25), indicating supersaturation. Variability was higher in the control mesocosms than in those containing clams. Although the mesocosms had different D.O. levels, various multiple comparison tests indicated that D.O. levels in the mesocosms were not significantly different from one another.

Dissolved oxygen (D.O.) levels ranged from a minimum of 8.1 mg L⁻¹ to a maximum of 13.5 mg L⁻¹ over the course of the summer sampling (Figure 26). At these water temperatures, D.O. levels were supersaturated. Multiple comparison tests indicated that there were no significant differences ($p < 0.05$) in D.O. levels among any of the mesocosms.

Dissolved oxygen (D.O.) levels can be strongly influenced by both physical (wind, water temperature) and biological processes (photosynthesis and respiration). Pearson correlation coefficients (r) of 0.68 (control), 0.57 (clams), 0.62 (clams+fish), and 0.68 (fish), all suggest that the association between water temperature and D.O. was significant at $p < 0.05$ during the spring experiment. Nonparametric correlation coefficients (Kendall's tau_b and Spearman's rank) revealed that the relationship between water temperature and D.O. was significant ($p < 0.01$) in all mesocosms at all times of the year. Is water temperature

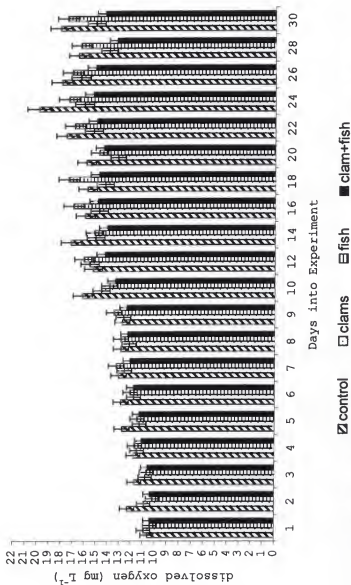


Figure 25. Changes in mesocosm dissolved oxygen during the spring experiment. Error bars represent 95% confidence intervals.

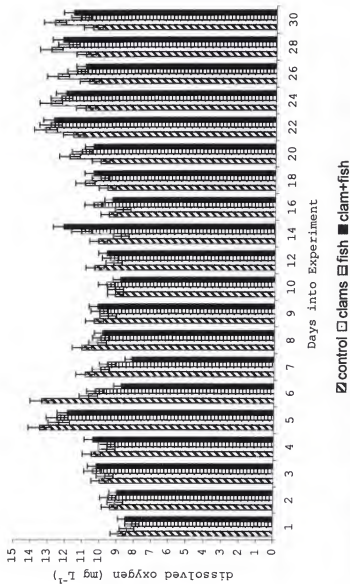


Figure 26. Changes in mesocosm dissolved oxygen during the summer experiment. Error bars represent 95% confidence intervals.

the determining factor of D.O. levels or is it photosynthesis, or a combination of the two? This question will be addressed in more detail when the relationship with phytoplankton is examined.

Would increased respiration from *Corbicula* suppress D.O. levels? Would pseudofeces produced by *Corbicula* suppress D.O. levels as aerobic microbes begin to break down these sheaths? We noted that although not significant over the entire sampling period, D.O. levels in the clam mesocosms were consistently lower than the other treatments in the winter (Figure 24) and spring (Figure 25) during the latter half of both experiments (days 12-30). Doering et al. (1986) found that clams, by stripping particles out of the water column and depositing them on the sediment, tended to lower D.O. levels in marine mesocosms due to the oxygen required for breakdown of the material by microbial activity. Similar results have been reported by Way et al. (1989) in assessing the distribution of *Corbicula* in the Tennessee River, where isolated pools containing clams generally had lower D.O. levels than the surrounding water outside the pools.

Microcosms containing fish as described by Flamarique-
Novalés et al. (1993) were found to have lower D.O. levels
due to excretion and also higher turbidity due to greater
levels of activity. Importantly, the competition for space
and lowering of D.O. on lake bottoms through biodeposition
by *Corbicula* could have negative impacts on fish eggs that
are deposited on lake and river bottoms (Zale 1987).

Phytoplankton (as Chlorophyll-a)

Chlorophyll concentrations all dropped over the course
of the winter sampling period but at very different
magnitudes (Figure 27). Both Figure 27 and results from
Wilcoxon Signed Ranks Test show chlorophyll-a levels in the
mesocosms containing clams were always lower than those of
the fish treatment and 85% of the time when compared to the
control and clams+fish treatments. Multiple comparison
tests confirmed that chl-a in the mesocosms containing only
clams were significantly lower than the control ($p=0.003$),
clams+fish ($p=0.023$), and fish ($p=0.001$) treatments over the
sampling period. Mesocosms containing clams (clams only as
well as clams+fish) had significantly lower chl-a levels
than the non-clam treatments (control, fish). Multiple
comparison tests all indicated that clam treatments were

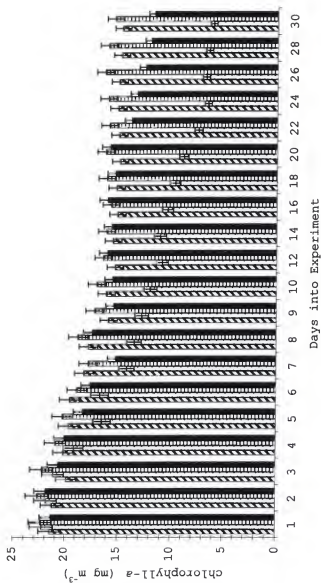


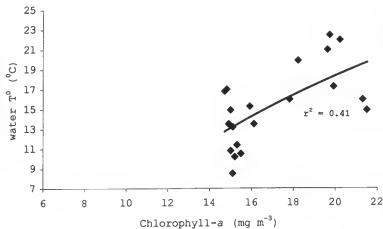
Figure 27. Changes in mesocosm chlorophyll-a during the winter experiment. Error bars represent 95% confidence intervals.

significantly lower during the winter experiment than both the control ($p=0.015$) and the fish ($p=0.001$), but not the clams+fish ($p=0.523$). This suggests that *Corbicula* were able to reduce phytoplankton concentrations significantly at winter temperatures more than in the mesocosms containing only zooplankton grazers (control) as well as zooplankton and fish grazers (fish).

There was little relationship between mesocosm water temperature and phytoplankton concentration (Figures 28a and 28b), likely indicating that reductions in phytoplankton are due more to biotic (grazing) than abiotic (temperature, photoperiod, nutrient availability, sinking) factors. As the strongest linear regression ($r^2= 0.41$) was found in mesocosms with the lowest number of grazers (control), this further supports this hypothesis.

. (McMahon (1979), Sickel (1986), and Lauritsen (1986a) found that the feeding rates of *Corbicula* were still substantial (>250 mL clam/hr) at winter temperatures above 7°C (Way et al. 1990) and that these mollusks are usually not thermally shocked until subjected to temperatures in the 3°C - 4°C range. Conversely, Shafland and Pestrak (1982) demonstrated that *Oreochromis* greatly reduced feeding

Control Mesocosms



Clam Mesocosms

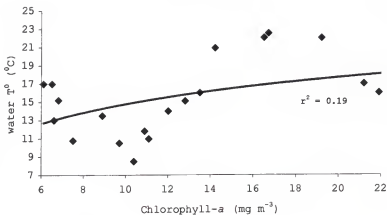
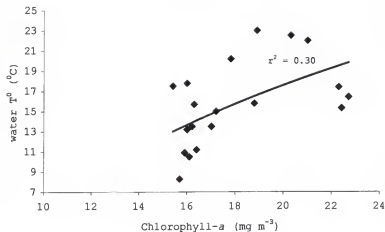


Figure 28a. Relationship between mesocosm water temperature and phytoplankton (chl-a) during the winter experiment.

Fish Mesocosms



Clams+Fish Mesocosms

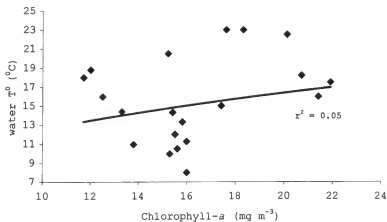


Figure 28b. Relationship between mesocosm water temperature and phytoplankton (chl-*a*) during the winter experiment.

between 13°C-16°C, stopped feeding between 10°C-12°C, lost equilibrium and body functions between 7°C-8°C, and usually died between 6°C-7°C. As winter water temperatures in the mesocosms were in the "reduced" feeding or "stopped" feeding range for about one half of the winter experiment (Figure 21), phytoplankton would be either free from or at reduced risk of predation by *Oreochromis*. However, this would not be true in the clam treatments and the reduced chl-*a* levels in these treatments verified this.

Corbicula have been found to be able to survive in most areas that do not have icy conditions for prolonged (weeks) periods of time (McMahon 1982). It is therefore obvious that not only will *Corbicula* survive in any water body in Florida (including the Panhandle), clam filtration rates should remain high. Although *Oreochromis* has survived temperatures dropping to 2.8°C for a few hours (Habel 1975), their physiological state is severely stressed below 6.5°C (Shafland and Pestrak 1982). While they are likely to survive in all parts of Florida, it would seem that their ability to feed and affect planktonic communities would be insignificant during the winter months in the northern and Panhandle areas of the state.

The presence of phytoplankton in all mesocosms increased as the spring days lengthened and the water began to warm up. The beginning and ending chl-a levels, however, differed markedly among the different treatments (Figure 29). Variability of chl-a was very pronounced in the control and fish treatments but much more suppressed in the treatments containing the filter-feeding clams. Mesocosms containing clams (clams, clam+fish) had lower chl-a values 90%-95% of the time compared with treatments containing no clams (control, fish) (Figure 29 and results from Wilcoxon Signed Rank Tests). Multiple comparison tests revealed that chl-a levels in the clam treatments were significantly lower than both the control and fish treatments ($p < 0.05$). The treatments containing both clams and fish (clam+fish) were also significantly lower ($p < 0.05$). These results strongly suggest that *Corbicula* exerts a strong negative impact on small suspended particles in the water column and phytoplankton under spring water temperatures (17°C - 29°C).

As the optimal filtering capacity of *Corbicula* occurred in water temperatures between approximately 22°C - 27°C (McMahon 1983), these clams were undoubtedly filtering and retaining significant amounts of phytoplankton cells.

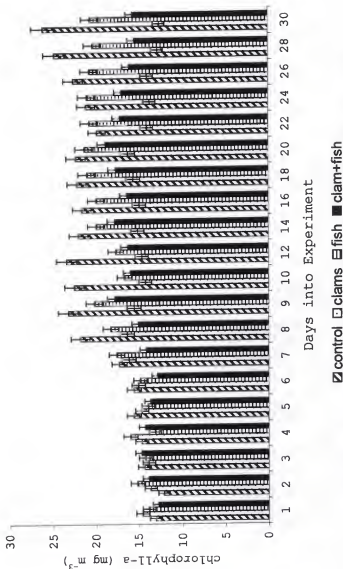


Figure 29. Changes in mesocosm chlorophyll-a during the spring experiment. Error bars represent 95% confidence intervals.

Although *Oreochromis* can consume large amounts of phytoplankton and detritus during the warmer spring months (Drenner et al. 1984, Zale and Gregory 1990, Cailteux et al. 1992), chl-a levels in the clam treatments were significantly lower ($p=0.012$) than the fish treatments. As chl-a levels were always lowest in the mesocosms containing clams, this suggested that *Corbicula* were able to filter larger volumes of water and retain phytoplankton cells more than *Oreochromis* under these particular thermal conditions.

Fish mesocosms had lower chl-a levels when compared to clam mesocosms 85% of the time, control mesocosms 90% of the time, and 100% of the time compared to the clams+fish mesocosms during the summer experiment (Figure 30 and results from Wilcoxon Signed Ranks Test). This may be explained in two ways. First, *Oreochromis* were able to filter and retain large amounts of phytoplankton (Anderson 1982, Drenner et al. 1987, Zale and Gregory 1990, Cailteux et al. 1992) at these warm water temperatures. This would suppress chlorophyll-a levels in the fish treatments. Conversely, *Corbicula* becomes severely stressed at water temperatures $>30^{\circ}\text{C}$ (Way et al. 1990). At these upper temperature levels, *Corbicula* tend to stop feeding (McMahon

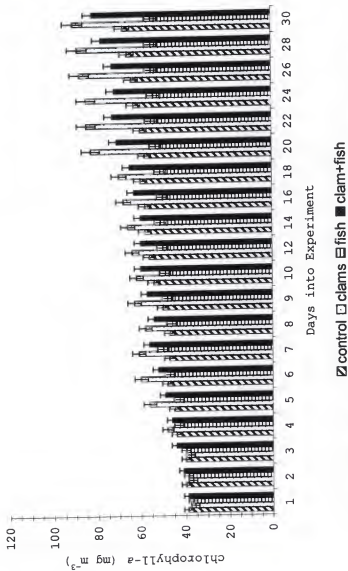


Figure 30. Changes in mesocosm chlorophyll-a during the summer experiment. Error bars represent 95% confidence intervals.

1979), and high mortality (indicated by a gape in the shell) occurs (Sickel 1986). With clam mortality comes visceral decay (as observed floating throughout the water column) in the clam and clam+fish mesocosms. It is suggested that decaying clam tissue released additional nutrients into the water column where it was readily assimilated by phytoplankton (as evidenced by the significant increases in chlorophyll-a concentrations in the mesocosms containing clams).

As noted during the winter and spring experiments, the relationship between water temperature and phytoplankton was also relatively weak during the summer sampling period ($r^2 = 0.55$). Highest chlorophyll-a concentrations were observed at times of the lowest water temperatures during the stressful summer sampling period. However, it is not suggested that water temperature alone controlled phytoplankton biomass during the summer as zooplankton grazing is likely important during this time as well.

A number of processes that are associated with dense populations of filter-feeding mollusks have a significant potential to affect water quality. These include high excretion rates associated with nonselective feeding and

nutrient cycling (Lauritsen and Mozley 1989), selective particle retention (Lauritsen 1986a), and increased respiration (Dame et al. 1991). Perhaps most importantly is that by efficient filter-feeding, *Corbicula* may actually shift trophic state toward oligotrophy as based on nutrient concentrations, water clarity, and chlorophyll-a. An example of this is the suggestion that *Corbicula* has triggered system-level changes in biota of the Potomac River, including increases in submerged aquatic vegetation (SAV), birds, and fish (Phelps 1994). It is likely that increased water clarity resulting from the enormous capacity of *Corbicula* to remove seston from the water column would increase the depth of the photic zone (Renata and Mackie 1994). This is the rationale behind the increase in SAV in the Potomac River since establishment of the mollusk.

Because of the ability of *Corbicula* to filter and retain or deposit phytoplankton cells to the benthos, one may hypothesize that primary production and biomass of phytoplankton will increase over time. However, the results just reported in this chapter have demonstrated that this was not the case. Therefore, the H_0 that there would be no significant differences in chlorophyll-a concentrations

between the control and the clam-containing and fish-containing mesocosms was rejected.

In this experiment, *Corbicula* had altered the entire pelagic-benthic energy balance in the mesocosm. A water column that was once driven by energy derived from the pelagic was transformed to energy derived from the benthos.

As is now being feared in the Great Lakes (Renata and Mackie 1994), this transformation may disrupt plankton food webs and ultimately fisheries.

Zooplankton

A total of 10 rotifer, 5 cladoceran, and 3 copepod taxa were identified from mesocosms over the course of the year-long experiment (Table 2). Although seasonal dynamics caused slight differences in zooplankton taxa in the mesocosms over the course of the experiment's wide range of water temperatures (between 7°C and 33°C), the rotifers *Keratella americana* and *Trichocera multicroinis*, the cladoceran, *Eubosmina tubicens*, calanoid copepod, *Diaptomus dorsalis*, and cyclopoid copepod, *Tropocyclops prasinus*, were numerically dominant throughout the mesocosm experiment.

There are several important differences in tropical zooplankton compared to their temperate counterparts.

Table 2. Rotifer, Cladoceran, and Copepod taxa identified in the mesocosm experiments

ROTIFERS

<i>Asplancha girodi</i>	<i>Keratella americana</i>
<i>Brachionus angularis</i>	<i>Keratella quadrata</i>
<i>Brachionus calyciflorus</i>	<i>Polyarthra vulgaris</i>
<i>Brachionus caudatus</i>	<i>Trichocera multicrinis</i>
<i>Conichilus dossuarius</i>	<i>Trichocera similis</i>

CLADOCERA

<i>Ceriodaphnia reticulata</i>	<i>Diaphanasoma brachyurum</i>
<i>Chydorus sphaericus</i>	<i>Eubosmina tubicens</i>
<i>Daphnia ambigua</i>	

COPEPODS

<i>Cyclops vernalis</i>	<i>Tropocyclops prasinus</i>
<i>Diaptomus dorsalis</i>	

Freshwater zooplankton are far less diverse in the tropics than in temperate areas (Gilwicz 1990). Highly efficient zooplanktivorous fishes such as *Oreochromis* (Fernando 1994) control tropical zooplankton. Tropical zooplankton are smaller in size than in the temperate zone due to continuous herbivorous predation (Fernando 1994) and metabolic costs associated with higher water temperatures (Lehman 1988). The large filter-feeding cladocerans found in temperate waters that suppress phytoplankton and small-bodied zooplankton such as *Daphnia magna* (Carpenter 1987) are absent from Florida lakes (Crisman and Beaver 1990).

The cornerstone assumption of controlling phytoplankton in lake biomanipulation experiments is that large-bodied cladoceran and copepod herbivores are capable of suppressing algal densities if they are freed from fish predation (Shapiro and Wright 1984, Dawidowicz 1990). In other words, oligotrophication is assumed to occur if predatory planktivores are either removed or kept at low levels (McQueen et al. 1986, Drenner et al. 1987). Most of the experimental work testing this hypothesis has been done in temperate systems (Shapiro and Wright 1984, Lampert 1988, Dawidowicz 1990, He et al. 1994). Because of differences in

zooplankton and fish communities of temperate versus tropical lakes as described by Crisman and Beaver (1990) and Fernando (1994), biomanipulation of tropical waters utilizing methods refined in temperate systems may not be applicable.

The assessment of zooplankton changes described in the remainder of this chapter attempted to test the classical pattern of cascading trophic interactions described by Carpenter et al. (1985), where piscivorous fish were absent in six mesocosms, allowing zooplankton to increase presumably with a subsequent reduction in phytoplankton biomass. The addition of filter-feeding *Corbicula* and the highly efficient zooplanktivorous *Oreochromis* (Fernando 1994) make this research different and unique to tropical systems.

Rotifers

Rotifers are able to consume dinoflagellates and smaller ciliated protozoans, thereby making them extremely important in energy transfer up the food chain to crustacean zooplankton and teleost fish (Fernando 1994). Because of their abundance in eutrophic environments (Schoenberg and Carlson 1984), rotifers represent a very important link in

the aquatic food chain. Rotifers are able to utilize nanoplankton and picoplankton and pass this energy along to larger cladocerans, copepods, and larval fish (Fernando 1994).

Rotifers tend to respond more quickly to environmental perturbations than do cladocerans and copepods (Gannon and Steinberger 1978), in part due to their short life cycle (capable of turning over every five days). Several studies have shown that by closely monitoring rotifer community dynamics, they can serve as a sensitive indicator of changes in water quality and predation (Gannon and Steinberger 1978, Fernando 1994). This approach proved effective in the Great Lakes, where dramatic changes in phytoplankton and rotifer biomass were observed, before the discovery of the cause of the decline (an introduced, highly predaceous cladoceran).

Changes in rotifer biomass were assessed to ascertain their importance as grazers on phytoplankton cells and as food for cladocerans, copepods, clams, and fish. Rotifer biomass ($\text{mg dw}^{-1} \text{ m}^{-3}$) remained relatively stable in mesocosms containing *Corbicula* and *Oreochromis* during the first half of the winter sampling period and steadily declined thereafter (Figure 31). Multiple comparisons tests



Figure 31. Changes in mesocosm rotifer biomass during the winter experiment. Error bars represent 95% confidence intervals.

revealed that mesocosms containing both clam+fish were significantly lower ($p=0.007$) than the control but not significantly lower than those containing only clams ($p=0.801$) or fish ($p=0.636$).

Biomass was significantly lower in both mesocosms containing just fish ($p=0.009$) and clams+fish ($p=0.001$) compared with the control. Rotifers also tended to be correlated significantly with phytoplankton levels in mesocosms containing only clams ($r=0.77$) and clams+fish ($r=0.73$). To test the strength of this correlation, linear regression models were run. These models indicated that although significantly correlated, the association between rotifer biomass and phytoplankton levels was actually relatively weak (Figures 32a, 32b).

Although *Oreochromis* predation may be reduced at winter water temperatures, the fact that rotifers significantly declined in the mesocosms containing fish suggests that grazing by *Oreochromus* played an important factor. Zale and Gregory (1990) found that rotifers (especially *Keratella*) were the most common item ingested by *Oreochromis*, constituting 23%-80% of their diet.

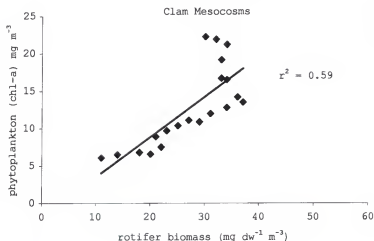
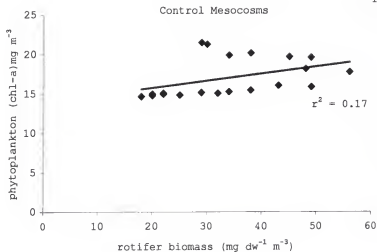
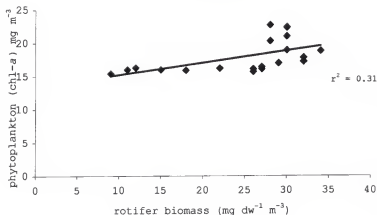


Figure 32a. Relationship between rotifers and phytoplankton during the winter sampling period in the control (top) and clam (bottom) mesocosms.

Fish Mesocosms



Clam+Fish Mesocosms

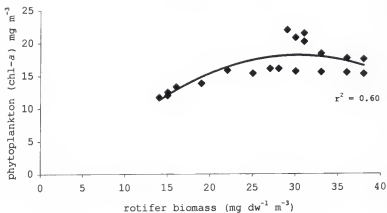


Figure 32b. Relationship between rotifers and phytoplankton during the winter sampling period in the fish (top) and clam+fish (bottom) mesocosms.

Although direct filtration of rotifers by *Corbicula* may not be significant when compared to phytoplankton feeding, rotifers do constitute a portion of their diet (McMahon 1983), and their biomass was significantly lower when compared to the control, indicating that *Corbicula* did prey on these organisms. The decline in rotifer biomass in the presence of filter-feeding predators is consistent with the previous work of Neil (1984) and Wu and Culver (1991).

As photoperiod increased during the spring sampling period, both water temperatures (Figure 22) and phytoplankton increased (Figure 29). Rotifer biomass also tended to increase in all mesocosms during the first week of the experiment but gradually decreased at different rates over the last three weeks (Figure 33). Over the course of the entire month, rotifer biomass in mesocosms containing *Oreochromis* (fish, clam+fish) was significantly lower ($p < 0.01$) than the control or *Corbicula* mesocosms. At the end of the experiment, rotifer biomass in all mesocosms (clam, fish, clam+fish) was significantly lower than the control (Figure 33). Mesocosms containing only clams were not significantly different than the clams+fish ($p = 0.087$) or fish ($p = 0.337$), indicating that *Oreochromis* and *Corbicula*

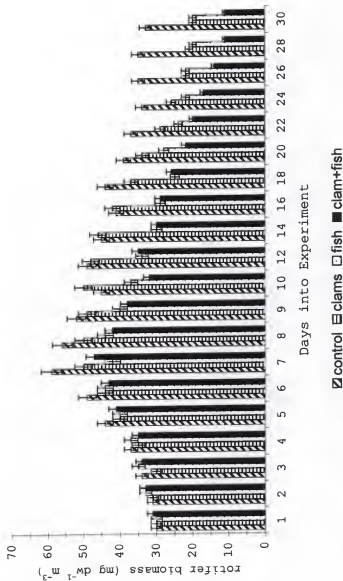


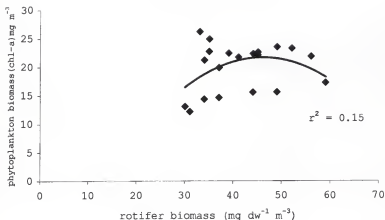
Figure 33. Changes in mesocosm rotifer biomass during the spring experiment. Error bars represent 95% confidence intervals.

were both effectively grazing on these organisms and reducing their biomass.

Gilwicz (1990) found that phytoplankton are usually reduced in eutrophic lakes by grazers only at the beginning of the spring growing season. Presumably, continued and efficient grazing diminishes once phytoplankton communities become dominated by filamentous cyanobacteria (Shapiro and Wright 1984, Threlkeld 1988). When they dominate eutrophic systems, one may expect that large-bodied zooplankton would be replaced by small-bodied cladocerans and rotifers (Lampert 1988). In this experiment, however, rotifers clearly declined (Figure 33), in part, from effective predation by *Oreochromis* and by being retained by the filter-feeding *Corbicula*.

Most rotifers are omnivorous, feeding on bacteria, protozoa, and phytoplankton (Gannon and Stemberger 1978, Gilbert 1989). If rotifers had any impact on reducing phytoplankton levels during the spring experiment, one would expect to see a negative correlation. Clearly, no significant correlation between rotifers and phytoplankton existed in the control or clam mesocosms (Figure 34a). Only in mesocosms containing fish did there appear to be a

Control Mesocosms



Clam Mesocosms

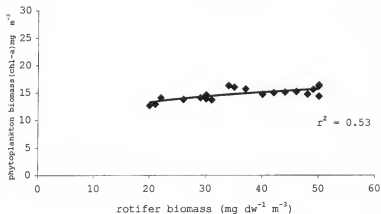


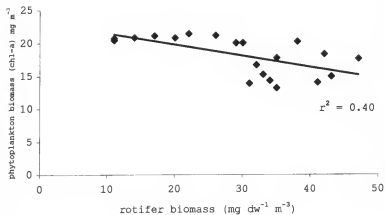
Figure 34a. Relationship between rotifers and phytoplankton during the spring sampling period in the control (top) and clam (bottom) mesocosms.

slight, but insignificant, negative correlation (Figure 34b). The fact that this negative correlation was only seen where *Oreochromis* was present (albeit, a very weak correlation) may lend credence to the idea that phytoplankton and rotifer biomass were significantly lower in the fish mesocosms because of predation.

Fernando (1994) found young herbivorous tilapias can significantly reduce rotifers in shallow littoral areas of tropical lakes. This, along with the ability of filter-feeding *Corbicula* to retain rotifers (McMahon 1983), is the likely reason that the mesocosms containing both clams and fish consistently had significantly lower phytoplankton and rotifer communities during the spring experiment.

Photoperiod, water temperature (Figure 23), phytoplankton (Figure 30), and rotifer biomass (Figure 35) all reached their highest levels of the one-year experiment during the summer experiment. Rotifer biomass increased in all mesocosms during the summer months. Rotifer biomass in the control mesocosms increased from approximately $50 \text{ mg dw}^{-1} \text{ m}^{-3}$ to $80 \text{ mg dw}^{-1} \text{ m}^{-3}$ (+60%), from $50 \text{ mg dw}^{-1} \text{ m}^{-3}$ to $90 \text{ mg dw}^{-1} \text{ m}^{-3}$ (+80%) in the clam mesocosms, and from $50 \text{ mg dw}^{-1} \text{ m}^{-3}$ to $85 \text{ mg dw}^{-1} \text{ m}^{-3}$ (+70%) in the mesocosms containing both

Fish Mesocosms



Clam+Fish Mesocosms

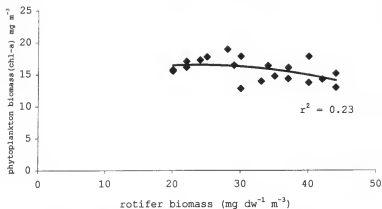


Figure 34b. Relationship between rotifers and phytoplankton during the spring sampling period in the fish (top) and clam+fish (bottom) mesocosms.

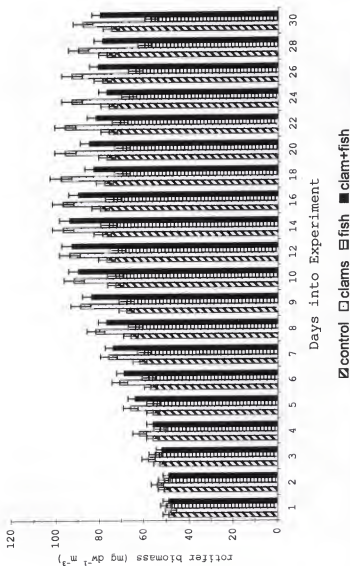


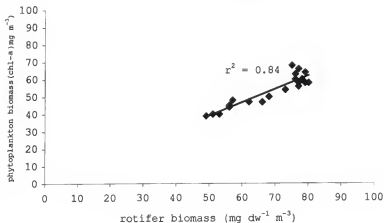
Figure 35. Changes in mesocosm rotifer biomass during the summer experiment. Error bars represent 95% confidence intervals.

clams and fish. In the mesocosms containing only fish, rotifer biomass increased less, from and $50 \text{ mg dw}^{-1} \text{ m}^{-3}$ to $60 \text{ mg dw}^{-1} \text{ m}^{-3}$ (+20%).

There was a significant positive correlation between phytoplankton levels and rotifer biomass in the control ($r=0.92$), clam ($r=0.81$), fish ($r=0.64$), and clam+fish ($r=0.70$) mesocosms. Figures 36a and 36b assess the strength of these relationships. Rotifer biomass in the control ($r^2=0.84$), clam ($r^2=0.67$), fish ($r^2=0.78$), and clam+fish ($r^2=0.37$) mesocosms were very similar, each increasing over the course of the 30 day experiment. This relationship confirms the fact that rotifer filtering is insignificant in controlling phytoplankton during the summer months.

Rotifer biomass in control mesocosms (Figure 35) was not significantly different than that in clam ($p=0.084$), or fish ($p=0.153$) mesocosms but was significantly lower ($p=0.008$) than that of the clam+fish mesocosms. *Corbicula* are thermally stressed at high water temperatures and actually seem to contribute to summer algal blooms (Figure 30). This contribution may be direct through death, with decay of their visceral tissue releasing nutrients into the water column to be utilized by phytoplankton quickly

Control Mesocosms



Clam Mesocosms

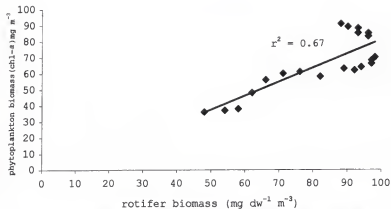
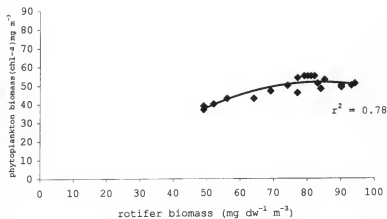


Figure 36a. Relationship between rotifers and phytoplankton during the summer sampling period in the control (top) and clam (bottom) mesocosms.

Fish Mesocosms



Clam+Fish Mesocosms

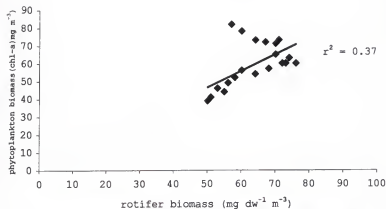


Figure 36b. Relationship between rotifers and phytoplankton during the summer sampling period in the fish (top) and clam+fish (bottom) mesocosms.

(Lauritsen and Mozley 1989). Therefore, it seems logical to observe that rotifers benefited from this increase in food availability (phytoplankton) in mesocosms containing clams (clams, clam+fish).

Although rotifer biomass in the fish mesocosms ended at significantly lower levels than the other mesocosms, multiple comparison tests indicated that the fish mesocosms were not significantly different from the control ($p=0.153$), clam ($p=0.941$), or clam+fish ($p=0.753$) mesocosms. The fish mesocosms were not significantly different from the control mesocosms until the last week (day 22-24) of the experiment. This closely corresponded with water temperatures dropping in the mesocosms from the 27°C-30°C range to 25°C (Figure 23), and may indicate a possible feeding response by *Oreochromis* to cooler water temperatures.

It is tempting to attribute the lowest rotifer biomass found at the end of the experiment in the fish mesocosms to predation. However, slight increases in rotifer numbers in the absence of fish were also found in Lake Wauberg and two areas of Lake Okeechobee (Crisman and Beaver 1990). As the variability of these increases were statistically insignificant when compared to where fish were present, it

appears that fish alone do not control rotifer populations (Gilbert 1989) and that predation from macrozooplankton may be equally important in regulating their abundance (Crisman and Beaver 1990, Fernando 1994).

Employing *in situ* enclosures in a Polish lake, Dawidowicz (1990) found that rotifers declined from 90% of total zooplankton biomass at the beginning of the experiment to only 18% at the end. The reduction in rotifers was followed by a decrease in phytoplankton abundance, thereby increasing water clarity. As fish were absent, in these enclosures, the increase in water clarity and decrease in small-bodied zooplankton (rotifers) was attributed to increased grazing by large herbivorous cladocerans and copepods. As this is the classical goal of any biomanipulation experiment in eutrophic waters (Schoenberg and Carlson 1984), the remainder of this chapter will evaluate whether this goal was achieved in the mesocosms.

Cladocerans and Copepods

The most important attribute of large cladocerans such as *Daphnia* and large omnivorous copepods such as *Diaptomus* in biomanipulation experiments is their ability to reduce algal biomass significantly if freed from fish predation

(Lynch 1979, Shapiro and Wright 1984). Most of these experiments have been conducted in temperate lakes (Shapiro 1990), where *in situ* enclosures containing *Daphnia* demonstrated effective control of small algae (Dawidowicz 1990). The results of several experiments completed in eutrophic temperate lakes have been encouraging, which prompted further testing of the manipulation of planktivory by the removal of planktivorous fish (He et al. 1994).

Several authors have questioned the relevance of these temperate lake experiments to subtropical ecosystems. Crisman and Beaver (1990) emphasized that subtropical lakes in Florida lack large-bodied cladocerans such as *Daphnia* and that fish assemblages in eutrophic lakes are dominated by pump filter-feeders rather than by the large temperate piscivores. Gilwicz (1990) found that large cladocerans couldn't grow and reproduce fast enough to control filamentous blue-green algae effectively. Most importantly, the presence of small-bodied rotifers, cladocerans, and herbivorous fishes in the tropics is in sharp contrast to the temperate large-bodied crustacean zooplankton and piscivorous predators (Fernando 1994). With smaller zooplankton (Lehman 1988, Fernando 1994) and pump filter-

feeding herbivorous fish, cladocerans and copepods can increase in abundance if freed from fish predation, but will likely have insignificant impacts on phytoplankton-dominated lakes (Crisman and Beaver 1990).

In this experiment, half (6) of the mesocosms freed cladocerans and copepods free from fish predation (control, clams), while the other half (6) had *Oreochromis* present. If the assumption that cladocerans and copepods reduce algal biomass if freed from fish predation is correct, one would expect that zooplankton biomass will significantly increase in the fishless mesocosms, thereby reducing phytoplankton (as chlorophyll-a) concentrations. It was the purpose of this experiment to put this cornerstone assumption of the biomanipulation approach to lake management to the test.

Cladoceran and copepod biomass increased in all mesocosms during the winter experiment but at very different levels (Figure 37). With biomass of cladocerans and copepods in all mesocosms at approximately $25 \text{ mg dw}^{-1} \text{ m}^{-3}$ at the beginning of the experiment, biomass increased 68% (control) and 65% (clam) in fishless mesocosms, as compared to 38% (fish) and 42% (clam+fish) in mesocosms possessing a planktivorous predator (*Oreochromis*). Nonparametric

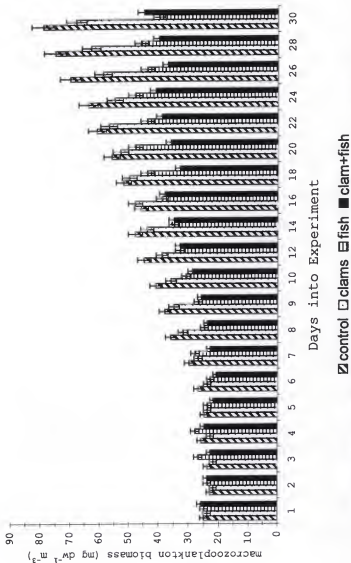


Figure 37. Changes in mesocosm macrozooplankton biomass during the winter experiment. Error bars represent 95% confidence intervals.

multiple comparison tests all indicated a significant difference ($p < 0.05$) between fishless and fish-containing mesocosms.

It appears that the assumption that cladoceran and copepod biomass would significantly increase if freed from fish predation was true during this sampling period. If this response is to be of any use in lake biomanipulation to increase water clarity, the significantly higher cladocerans and copepods must be able to reduce algal biomass effectively. There was no significant difference ($p > 0.05$) in phytoplankton (chlorophyll-a) in the control versus fish mesocosms (Figure 27). The clam mesocosms, however, exhibited significantly lower phytoplankton biomass than the control ($p = 0.003$), fish ($p = 0.001$), or clam+fish ($p = 0.023$) mesocosms. This would lead one to believe that it was *Corbicula*, not the dominant cladoceran (*Eubosmina tubicens*) or copepod (*Cyclops vernalis*) found in the mesocosms, which was most effective at grazing phytoplankton.

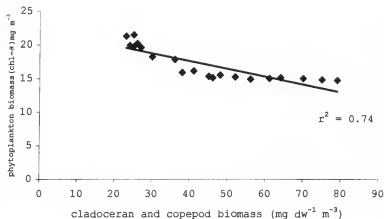
In Lakes Wauberg, Apopka, and Okeechobee, Crisman and Beaver (1990) found similar responses with an increase in cladoceran and copepod abundance in fishless treatments. Unlike the algal reduction that is normally found in

temperate lakes with significant increases in large-bodied zooplankton, algal biomass actually increased 9% to 31% in these three Florida lakes. With similar results, Schoenberg and Carlson (1984) began to question the value of small-bodied tropical zooplankton as an effective biomanipulation tool.

However, there was a strong negative correlation between the increase in cladoceran/copepod biomass and the decrease in phytoplankton (Figures 38a, 38b). Freed from predation, a significant negative correlation between phytoplankton and macrozooplankton existed in the fishless mesocosms, the control ($r=-0.86$) and clam ($r=-0.93$). Although less strong, significant negative correlations also existed in the fish-containing mesocosms, fish ($r=-0.77$) and clam+fish ($r=-0.76$) mesocosms. This certainly suggests that cladocerans and copepods exert a significant impact on phytoplankton. In all of the mesocosms, more so when they are free from fish predation

Cladoceran and copepod biomass was highest (Figure 37) and phytoplankton biomass lowest (Figure 27) in the clam mesocosms. These findings add credence to the hypothesis that filter-feeders (both zooplankton and mollusk) can

Control Mesocosms



Clam Mesocosms

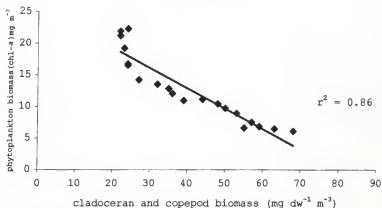
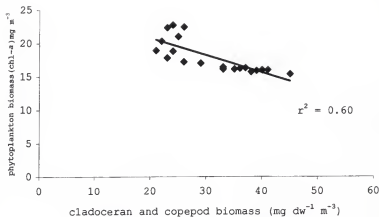


Figure 38a. Relationship between cladocerans and copepods and phytoplankton during the winter sampling period in the control (top) and clam (bottom) mesocosms.

Fish Mesocosms



Clam+Fish Mesocosms

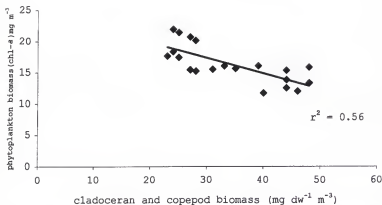


Figure 38b. Relationship between cladocerans and copepods and phytoplankton during the winter sampling period in the fish (top) and clam+fish (bottom) mesocosms.

control phytoplankton if freed from predation. As most biomanipulation experiments remove fish with the hope that cladocerans and copepods will increase (Shapiro and Wright 1984, Drenner et al. 1987, Beaver et al. 1994), this experiment suggests that greater control of phytoplankton might be realized if a molluscan component was added as well.

There was a significantly different ($p < 0.05$) response of cladoceran and copepod biomass in the fishless (control, clams) versus fish (fish, clams+fish) mesocosms during the spring sampling period (Figure 39). Biomass in the fishless mesocosms nearly tripled, from approximately $29 \text{ mg dw}^{-1} \text{ m}^{-3}$ at the beginning of the experiment to approximately $88 \text{ mg dw}^{-1} \text{ m}^{-3}$ at the end. In the mesocosms containing predatory fish, the increase was slight, from approximately $29 \text{ mg dw}^{-1} \text{ m}^{-3}$ to an average of about $50 \text{ mg dw}^{-1} \text{ m}^{-3}$.

With water temperatures between 17°C - 25°C during most of the spring sampling period (Figure 22), conditions were optimal for filter-feeding *Corbicula* (McMahon 1983). Phytoplankton biomass was lowest in the clam mesocosms during the spring (Figure 29), indicating that *Corbicula* filter-feeding was able to suppress phytoplankton and

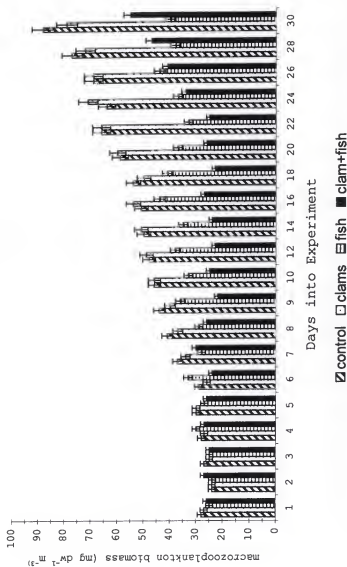


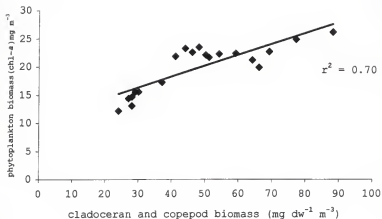
Figure 39. Changes in mesocosm macrozooplankton biomass during the spring experiment. Error bars represent 95% confidence intervals.

possibly rotifers (Figure 33) significantly at these water temperatures. However, filter-feeding by *Corbicula* clearly had no impact on suppressing the larger cladocerans and copepods (Figure 39).

Shafland and Pestrak (1982), Lazarro (1987), and Fernando (1994) all found that *Oreochromis* feeding rates tended to increase with increasing water temperature. As these studies have shown a positive correlation between water temperature and the feeding rate of *Oreochromis*, it was expected due to increased predation that fish-containing mesocosms would have significantly lower cladoceran and copepod biomass than fishless mesocosms during the spring experiment. This expectation was realized.

The only negative correlations found, albeit very weak, between phytoplankton and their grazers were those found in mesocosms containing *Corbicula*. Negative correlations of $r=-0.44$ and $r=-0.04$ were found in the clams and clams+fish mesocosms, respectively. On the other hand, in mesocosms where *Corbicula* were absent, positive correlations of $r=0.84$ (control) and $r=0.78$ (fish) were found. Cladocerans and copepods clearly did not suppress phytoplankton at spring photoperiods and water temperatures (Figures 40a and 40b).

Control Mesocosms



Clam Mesocosms

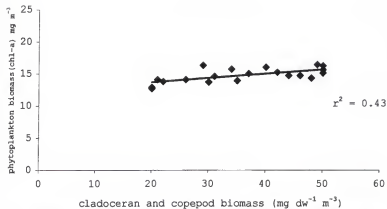
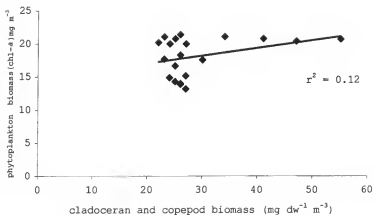


Figure 40a. Relationship between cladocerans and copepods and phytoplankton during the spring sampling period in the control (top) and clam (bottom) mesocosms.

Fish Mesocosms



Clam+Fish Mesocosms

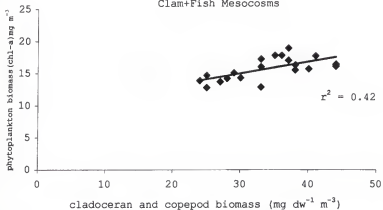


Figure 40b. Relationship between cladocerans and copepods and phytoplankton during the spring sampling period in the fish (top) and clam+fish (bottom) mesocosms.

With the fewest cladoceran and copepod grazers available (Figure 39), logic would dictate that these mesocosms would therefore contain the highest levels of phytoplankton. This scenario did not appear to be true, as phytoplankton in mesocosms containing fish were significantly lower ($p < 0.05$) than the control (Figure 29). This would certainly lead one to conclude that *Oreochromis* must also have a noticeable role in suppressing phytoplankton at these water temperatures in addition to that of herbaceous zooplankton. Higher rotifer, cladoceran, and copepod abundance (and presumably biomass) were found in fishless enclosures in several Florida lakes (Crisman and Beaver 1990). However, chlorophyll concentrations were similarly higher as well. These results suggest that while removal of planktivorous pump filter-feeding fish such as gizzard shad (*Dorosoma cepedianum*) results in higher macrozooplankton populations in subtropical lakes, phytoplankton are not reduced, as would be expected in this type of biomanipulation experiment. As the Crisman and Beaver experiment differed from mesocosm results just reported, this could lead one to conclude that *Oreochromis* must be a more effective algal grazer than *D. cepedianum*.

Another explanation may be the fact that *Oreochromis* fecal material completely suppressed algal production in cyanophytes and more than 60% in chlorophytes in laboratory experiments (Fernandes 1994). *D. cepedianum* feces, on the other hand, increased chlorophyll-*a* values in both algal groups (Fernandes 1994). As found by Threlkeld (1988) and supported by the Crisman and Beaver results, the potential benefits of fish planktivory can often be exceeded by water column nutrient release from inefficient feeding and high fecal organic matter.

With long photoperiods and warm water temperatures, cladoceran and copepod biomass increased in all mesocosms (Figure 41) during the summer. As has been found with other variables, the rate of this increase varied considerably among treatments. In the fishless mesocosms (control, clams), biomass increased from approximately $39 \text{ mg dw}^{-1} \text{ m}^{-3}$ to an average of approximately $130 \text{ mg dw}^{-1} \text{ m}^{-3}$ (+330%) by the end of the sampling period. In the fish-containing mesocosms (fish, clams+fish), however, this increase was from $39 \text{ mg dw}^{-1} \text{ m}^{-3}$ to approximately $90 \text{ mg dw}^{-1} \text{ m}^{-3}$ (+230%). With such a large increase in available filter-feeding zooplankton, one would expect that phytoplankton would be

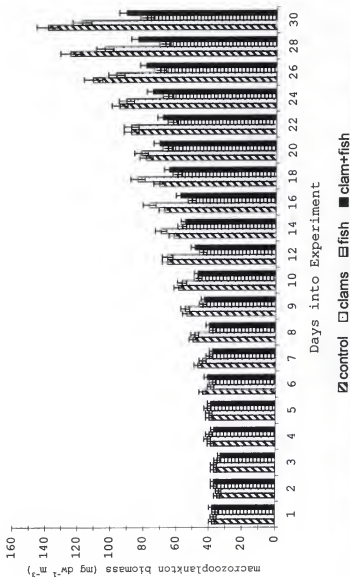


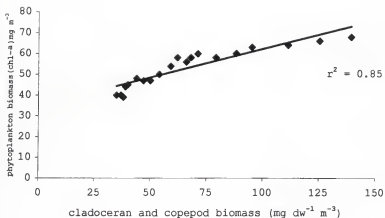
Figure 41. Changes in mesocosm macrozooplankton biomass during the summer experiment. Error bars represent 95% confidence intervals.

suppressed by zooplankton grazing. As has clearly be seen (Figure 39), such is not the case, as phytoplankton also increased in all mesocosms.

Strong positive Pearson correlation coefficients of $r=0.92$ (control), $r=0.93$ (clams), $r=0.85$ (fish), and $r=0.95$ (clams+fish) all indicate that phytoplankton and zooplankton are increasing at essentially a linear rate (Figures 42a and 42b), with no predator (*Corbicula* and/or *Oreochromis*) keeping the planktonic community suppressed.

No large differences in cladoceran/copepod biomass can be seen among the treatments throughout the first week of the experiment but there was a separation between the fishless mesocosms (control, clams) and the fish-containing mesocosms (fish, clams+fish) over the final 3 weeks (Figure 41). We observed that water temperature peaked on day 8 of the experiment (33°C) and gradually declined over the last 3 weeks of the experiment (Figure 23). This coincides with the same time that differences in cladoceran/copepod biomass in the fishless (control, clams) and fish-containing (fish, clams+fish) mesocosms began well. Nonparametric comparison tests indicated that no significant difference was found between the control and clam ($p=0.996$), fish ($p=0.157$), and

Control Mesocosms



Clam Mesocosms

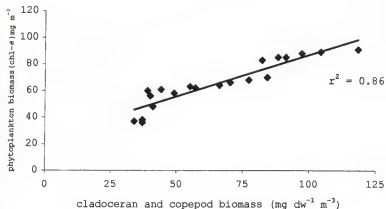
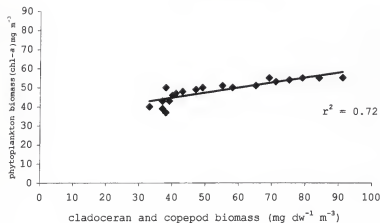


Figure 42a. Relationship between cladocerans and copepods and phytoplankton during the summer sampling period in the control (top) and clam (bottom) mesocosms.

Fish Mesocosms



Clam+Fish Mesocosms

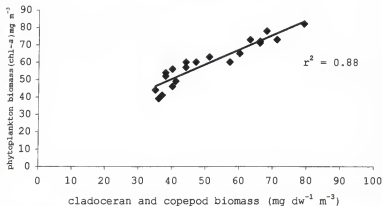


Figure 42b. Relationship between cladocerans and copepods and phytoplankton during the summer sampling period in fish (top) and clam+fish (bottom) mesocosms.

clams+fish ($p=0.384$) mesocosms over the entire 30 day sampling period, however.

Physiological stress (as measured by dissolved oxygen consumption and respiration) in *Corbicula* as water temperatures rose above 25°C has been described by McMahon (1979). Those *Corbicula* that survived at these water temperatures tended to cease feeding (shells tightly closed) due to thermal stress (Byrne et al. 1988). It has been found that *Corbicula*'s sensitivity to toxic stressors also greatly increased as water temperatures rose above 25°C-26°C range (Doherty and Cherry 1988). Throughout most of the summer experiment, it is therefore safe to assume that *Corbicula* were either non-feeding or dead. This seems to be confirmed by the fact that *Corbicula*'s preferred food (phytoplankton and small particles) was higher in the clam mesocosms than that found in the other three treatments (Figure 30).

It has been observed that zooplankton biomass similarly remained stable in sets of enclosures for the first week of incubation and increased rapidly over the remaining two weeks in water temperatures between 19.5°C and 22°C (Dawidowicz 1990). With both biomass and filtering rate of

cladocerans increasing in fishless enclosures over time, one would anticipate seeing a reduction in chlorophyll-a in accordance with the theoretical assumptions of biomanipulation approach. However, phytoplankton actually increased in the enclosures, which Dawidowicz (1990) attributed to the summer increase of filamentous blue-greens. Although macrozooplankton biomass usually increases over the summer months, Gilwicz (1990) found that most cladocerans tend to be much less efficient feeders if densities of blue-greens are high, as they tend to inhibit filtering rates. This would suggest that in enclosures where blue-greens comprise an insignificant portion of the phytoplankton assemblage, both cladocerans and copepods can be expected to greatly increase their biomass in response to the plentiful and palatable food available.

Similar increases in cladoceran abundance in fishless enclosures have been observed (Crisman and Beaver 1990). However, blue-green algae actually increased in both Lake Okeechobee experiments and remained unchanged in Lake Apopka. Despite increases in herbaceous cladocerans comparable to that observed in these mesocosm experiments, Schoenberg and Carlson (1984) observed that blue-greens

(*Microcystis*) dominated in many lakes. As blue-greens normally dominate hypereutrophic Florida lakes in summer (Bays and Crisman 1983, Brenner et al. 1991), it can therefore be expected that phytoplankton will increase regardless of any observable increase in the cladoceran and copepod communities.

In Polish and Swedish eutrophic lakes dominated by filamentous blue-greens such as *Oscillatoria*, *Lyngbya*, and *Aphanizomenon* (all present in Florida waters), Gilwicz (1990) observed that large-bodied filter-feeding species such as *Daphnia* decline in number and are soon replaced by small-bodied cladoceran and rotifer species. Laboratory studies have shown increased chlorophyll-*a* concentrations from approximately 40 $\mu\text{g L}^{-1}$ to 70 $\mu\text{g L}^{-1}$ during algal bloom formation (Lambert 1988). Presumably, inhibition of cladoceran filter-feeding by noxious warm water filamentous blue-greens causes this to occur. Similar observations have been described in Florida waters (Crisman and Beaver 1990).

As Florida lakes lack the large-bodied cladocerans (Crisman and Beaver 1990), smaller-bodied cladocerans and rotifers may actually increase in abundance (Figure 41), but their ability to suppress phytoplankton (especially

filamentous blue-greens) during summer months appears to be minimal (Figure 30). Because of this, several researchers (Crisman and Beaver 1990, Dawidowicz 1990, Gilwicz 1990, Fernando 1994) have questioned the ability of cladocerans to suppress phytoplankton even in the absence of planktivorous fish. Because filamentous blue-green algae (dominant in subtropical eutrophic lakes) inhibit feeding by cladocerans and copepods, phytoplankton may increase in subtropical and tropical waters regardless of whether predators increase as well. Therefore, biomanipulation techniques for eutrophication management in the subtropics and tropics must differ than proposed for temperate lakes. It has been shown in several subtropical and tropical experiments that simply removing planktivorous fish and allowing macrozooplankton predators to increase does not necessarily mean that phytoplankton (and trophic state) will decrease.

Summary

In order for zooplankton to be useful in reducing eutrophication in subtropical lakes, the abundance and biomass of the large-bodied herbivorous cladocerans and copepods must either increase over time or be sufficient to control the abundance of phytoplankton effectively (Gilwicz

1990, Crisman and Beaver 1990, Novales-Flamarique et al. 1993). In biomanipulation experiments, it is expected that abundant cladocerans and copepods are likely to reduce rotifer and nauplii biomass (Lane 1979) as well as control the level of phytoplankton abundance (Gilwicz 1990). During the winter sampling period, this classic trophic cascading approach was realized (Figures 43a, 43b). It is important to note, however, that cladoceran and copepod biomass increased in the fish mesocosms (fish, clams+fish), contrary to results in some subtropical (Crisman and Beaver 1990) and tropical (Fernando 1994) experiments, although the increase was less than that found in the fishless mesocosms (control, clams).

Cladocerans and copepods increased during the spring (Figures 44a, 44b) and summer (Figures 45a, 45b) sampling periods as well. The only treatment where phytoplankton decreased was during the spring sampling period and was found in the mesocosms containing clams. With an increase in herbivorous zooplankton and optimal water temperature (17°C - 24°C) for filter-feeding *Corbicula*, the combination of herbaceous zooplankton and filter-feeding clams were able to significantly decrease phytoplankton ($p=0.012$) compared to

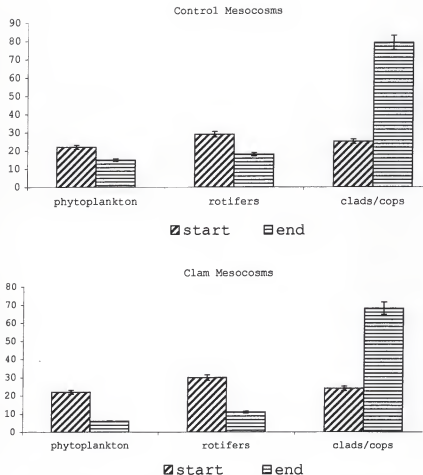
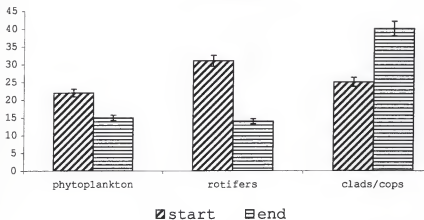


Figure 43a. Change in phytoplankton, rotifer, and cladoceran/copepod (clads/cops) biomass during the winter experiment in the control (top) and clam (bottom) mesocosms. Error bars represent 95% confidence intervals.

Phytoplankton values in mg m^{-3} and rotifers/clad/cops in $\text{mg dw}^{-1} \text{m}^{-3}$.

Fish Mesocosms



Clam+Fish Mesocosms

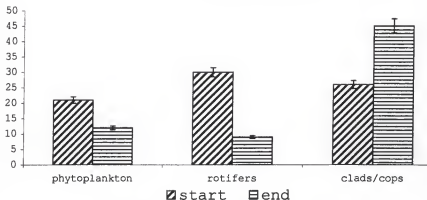
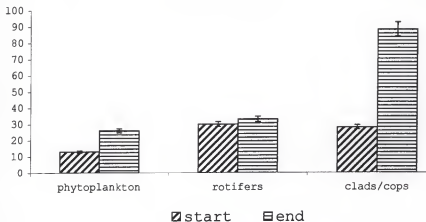


Figure 43b. Change in phytoplankton, rotifer, and cladoceran/copepod (clads/cops) biomass during the winter experiment in the fish (top) and clam+fish (bottom) mesocosms. Error bars represent 95% confidence intervals.

Phytoplankton values in mg m⁻³ and rotifers/clad/cops in mg dw⁻¹ m⁻³.

Control Mesocosms



Clam Mesocosms

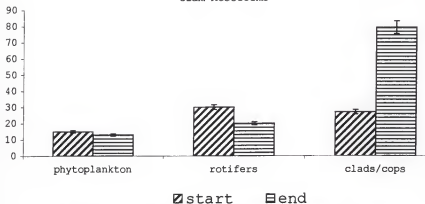
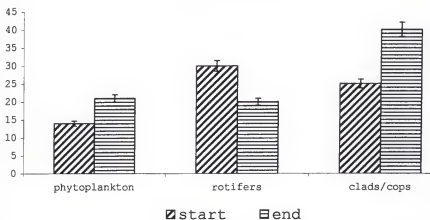


Figure 44e. Change in phytoplankton, rotifer, and cladoceran/copepod (clads/cops) biomass during the spring experiment in the control (top) and clam (bottom) mesocosms. Error bars represent 95% confidence intervals.

Phytoplankton values in mg m^{-3} and rotifers/clads/cops in $\text{mg dw}^{-1} \text{m}^{-3}$.

Fish Mesocosms



Clam+Fish Mesocosms

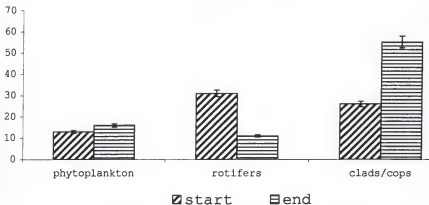


Figure 44b. Change in phytoplankton, rotifer, and cladoceran/copepod (clads/cops) biomass during the spring experiment in the fish (top) and clam+fish (bottom) mesocosms. Error bars represent 95% confidence intervals.

Phytoplankton values in mg m^{-3} and rotifers/clads/cops in $\text{mg dw}^{-1} \text{ m}^{-3}$.

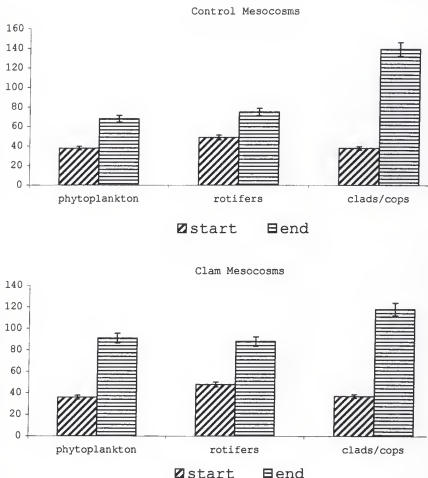
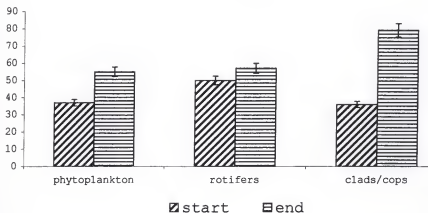


Figure 45a. Change in phytoplankton, rotifer, and cladoceran/copepod (clads/cops) biomass during the summer experiment in the control (top) and clam (bottom) mesocosms. Error bars represent 95% confidence intervals. Phytoplankton values in mg m⁻³ and rotifers/clads/cops in mg dw⁻¹ m⁻³.

Fish Mesocosms



Clam+Fish Mesocosms

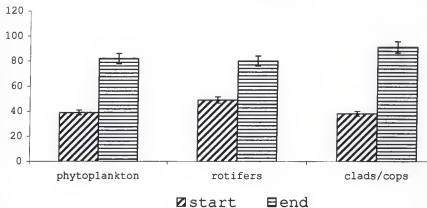


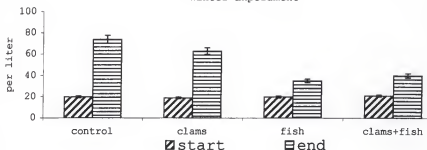
Figure 45b. Change in phytoplankton, rotifer, and cladoceran/copepod (clads/cops) biomass during the summer experiment in the fish (top) and clam+fish (bottom) mesocosms. Error bars represent 95% confidence intervals. Phytoplankton values in mg m^{-3} and rotifers/clads/cops in $\text{mg dw}^{-1} \text{m}^{-3}$.

fish-containing treatments. As the combination of filter-feeding macrozooplankton and clams appears to be very effective at suppressing phytoplankton under these thermal conditions, many temperate areas may wish to investigate adding a filter-feeding mollusk as a biomanipulation tool.

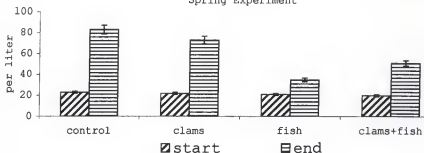
It was found that the abundance of the cladocerans *Daphnia ambigua* and *Eubosmina tubicens*, along with the copepod *Diaptomus dorsalis*, increased in Lake Denham (from 22 L⁻¹ to 150 L⁻¹) following removal of rough fish (primarily the gizzard shad, *Dorosoma cepedianum*) (Beaver et al. 1994). These results certainly suggest that an increase in crustacean zooplankton communities may be directly related to reduced predation pressure from planktivorous fish.

The increased abundance of crustacean zooplankton in the mesocosm experiments differed somewhat from that reported in Lake Denham. Average numbers of cladocerans and copepods increased throughout the year in all mesocosms (Figure 46), although clearly the magnitude of the increase was greater in fishless mesocosms (control, clams) than in mesocosms containing fish (fish, clams+fish). Part of this difference may be attributed to the degree of pressure that the Lake Denham planktivorous fish, *D. cepedianum* and

Winter Experiment



Spring Experiment



Summer Experiment

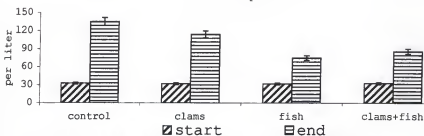
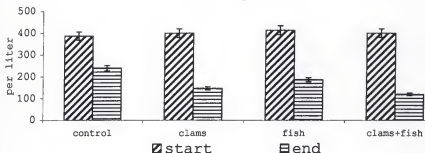


Figure 46. The average cladoceran and copepod abundance at the start and end of each experiment. Error bars represent 95% confidence intervals.

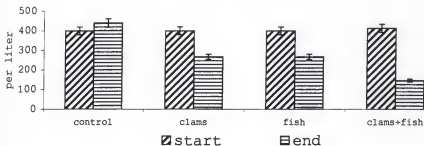
mesocosm blue tilapia, *Oreochromis aureus*, exerted on crustacean zooplankton. Although *Oreochromis* positively selects for copepodites and cladocerans in laboratory feeding experiments (Zale 1987), as much as 90% of their gut contents (volumetrically) can consist of phytoplankton and detritus (Zale 1990) as well as rotifers (Spaturu 1978). Therefore, lowered rotifer abundance at the end of each experiment (Figure 47) in mesocosms containing fish (fish, clams+fish), when compared to the fishless mesocosms (control, clams), can be attributed to predation of *Oreochromis* as well as grazing by cyclopoid crustaceans (Lane 1979). Similar responses of rotifers to fish predation have been reported by Carpenter (1987) and Gilbert (1989).

Because the physiology of filter-feeding is directly linked to water temperature (Jorgensen 1966, Foe 1986a, Lauritsen 1986b), the effectiveness of cladocerans, copepods, and clams in suppressing phytoplankton through their grazing seems to be seasonal in nature, even in the subtropics. The cooler winter and spring sampling periods saw significant increases in cladoceran and copepod biomass,

Winter Experiment



Spring Experiment



Summer Experiment

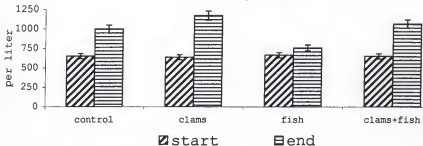


Figure 47. The average rotifer abundance at the start and end of each experiment. Error bars represent 95% confidence intervals.

resulting in declines (winter) or insignificant increases (spring) in phytoplankton. However, due to the shorter photoperiod and lower water temperatures, one may also expect phytoplankton levels to be lower in the winter and early spring, regardless of cladoceran and copepod abundance. During the hot summer months, thermal stress caused high *Corbicula* mortality and presumably the release of nutrients into the water column from visceral decay, quickly taken up by phytoplankton. Because of maximum photoperiod and available nutrients, phytoplankton increased significantly during the summer experiment. This appears that the use of an abundant filter-feeder such as *Corbicula* or *Oreochromis* may prove ineffective as a biomanipulation tool in reducing nutrient enrichment of Florida waters over a considerable portion of the year when water temperatures are warm ($>15^{\circ}\text{C}$).

Although O'Brien (1979), Anderson (1982), and Drenner et al. (1984) all documented the importance of fish predation on rotifers, cladocerans, and copepods, the reduction of algal biomass in the presence of enhanced cladoceran and copepod populations may not be seen in subtropical ecosystems (Crisman and Beaver 1990). However,

the addition of a high-volume filter-feeding mollusk such as *Corbicula* as part of a biomanipulation approach may aid in reducing algal biomass in Florida waters. As described by Wu and Culver (1991) and Mackie (1992), the addition of the zebra mussel (*Dreissena polymorpha*) in temperate systems has clearly demonstrated that abundant, high-volume, filter-feeding mollusks may suppress algal biomass more effectively than the now classical approach of biomanipulation in aquatic systems where macrozooplankton grazing is the determinant factor.

CHAPTER 7 CONCLUSIONS

Conclusion 1. In both microcosm and mesocosm experiments, *Corbicula* were able to significantly suppress phytoplankton (as chl-a) when water temperatures did not inhibit the clam's filtering ability due to thermal stress ($<30^{\circ}\text{C}$).

In outdoor mesocosms containing *Corbicula*, lower phytoplankton levels (chl-a) were found 90%-95% of the time when compared with mesocosms containing no clams under spring water temperatures (17°C - 29°C). During winter conditions (water temperatures between 7°C and 23°C), clam mesocosms had lower phytoplankton (chl-a) levels 100% of the time when compared with mesocosms containing fish and 85% of the time when compared to the control mesocosms. However, under thermally stressed summer conditions where water temperatures were 30°C - 33°C , chl-a levels in the clam-containing mesocosms were significantly higher than the control or fish mesocosms.

Conclusion 2. In the laboratory experiments where water temperatures were 22°C and 24°C , optimal for filter-feeding, turbidity levels were significantly lower in microcosms containing *Corbicula* when compared to the control.

Where successfully established in Florida, *Corbicula* and *Oreochromis* usually comprise a significant component of the aquatic ecosystem (Belanger et al. 1990, Brenner et al. 1991, Nordlie 1991, Hale et al. 1995). Because of the clam's high filtration rates (Lauritsen 1986a, Way et al. 1990), nonselective feeding (Foe 1985, Lauritsen 1986b), and high abundance (Kraemer 1979, McMahon 1982), *Corbicula* are able to reduce the number of small particles found in the water column significantly (Cohen et al. 1984, Foe 1985), sometimes causing dramatic ecological changes (Officer 1982, Phelps 1994).

The success of *Oreochromis* in colonizing new systems and rapidly achieving high abundances in Florida (Zale 1987) may be attributed to several unique life-history characteristics (such as mouth brooding), and the ability to feed effectively on phytoplankton and microzooplankton (Zale 1990). *Oreochromis* has displaced the recreationally popular largemouth bass (*Micropterus salmoides*) in many of Florida's lakes (Hale et al. 1994). Importantly, *Oreochromis* suppresses phytoplankton biomass (especially blue-greens) in laboratory experiments (Fernandes et al. 1994), making them more effective in reducing algal biomass

compared to the inefficient pump filter-feeder, gizzard shad (*Dorosoma cepedianum*).

Conclusion 3. Rotifer, cladoceran, and copepod biomass were significantly higher in fishless-containing mesocosms (control, clams) than those containing fish (fish, clams+fish).

From pooling all data from the year-long experiment, we see that (a) there were significantly more cladocerans and copepods (biomass) in the control mesocosms compared to the fish (ANOVA: $F=14.25$; $df=1,118$; $p=0.0003$) and clams+fish (ANOVA: $F=15.23$; $df=1,118$; $p=0.0002$); (b) there were significantly more cladocerans and copepods (biomass) in the clam mesocosms compared to the fish (ANOVA: $F=11.06$; $df=1,118$; $p=0.001$) and clams+fish (ANOVA: $F=12.10$; $df=1,118$; $p=0.001$); (c) there were significantly more rotifers (biomass) in the control mesocosms when compared to the fish (ANOVA: $F=4.63$; $df=1,118$; $p=0.03$) and nearly a significant difference in the clam mesocosms compared to the fish (ANOVA: $F=3.48$; $df=1,118$; $p=0.06$); and (d) no significant differences in phytoplankton levels were found in any of the mesocosms after pooling all of the one-year data (Figure 48).

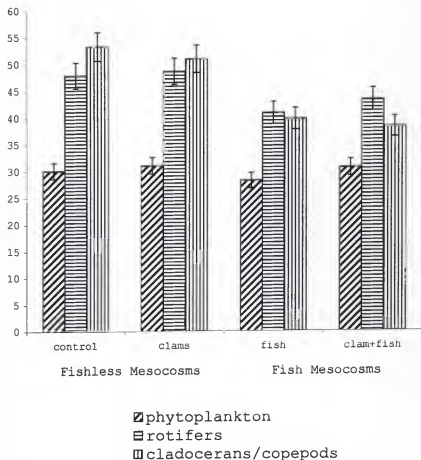


Figure 48. Comparison of pooled data in all mesocosms after one year of sampling.

Error bars represent 95% confidence intervals.

Phytoplankton values are in mg m^{-3} and rotifers/cladocerans/copepods in $\text{mg dw}^{-1} \text{m}^3$.

Results presented here and by other subtropical investigators question the value of whole lake experiments that just remove fish with the objective of increasing water quality through increased zooplankton grazing. Algal biomass was clearly suppressed in *Corbicula* mesocosms when water temperatures did not exceed 28°C, signifying that the exotic mollusk may be an effective eutrophic control throughout most of the year. To maximize the chance of achieving increased water clarity by biomanipulative means, a benthic filter-feeding component should be added as it is clear that small-bodied cladocerans found in Florida waters are not able to suppress algal biomass on their own. In the experimental results just presented, water clarity "improved" most significantly in the mesocosms containing both the fish **and** the clams. This combination should be considered when planning whole lake biomanipulation experiments in the future.

For *Corbicula* and *Oreochromis* to be effective algal controls in Florida waters, filter-feeding cladocerans and copepods must increase, and the whole community must be able to suppress phytoplankton biomass. Freed from

predation, cladoceran and copepod biomass were higher in the fishless mesocosms (control, clams) than the fish-containing mesocosms (fish, clams+fish). Although macrozooplankton increased in fishless mesocosms, the classical biomanipulation pattern of cascading trophic interactions where increased zooplankton grazing populations significantly reduce phytoplankton biomass was not realized.

These results reaffirm what have been previously reported in similar subtropical investigations (Schoenberg and Carlson 1984, Crisman and Beaver 1990, Beaver et al. 1994). Because of their reduced size compared to temperate systems (Crisman and Beaver 1990), even when cladocerans and copepods significantly increase, Florida's small-bodied assemblages are not able to effectively suppress algal communities. Therefore, the classical approach of removing planktivorous fish to encourage increases in zooplankton populations is of questionable value as a biomanipulation tool in eutrophic subtropical waters.

Corbicula and *Oreochromis* are firmly established in Florida waters. As both exotics are very effective at removing smaller-bodied phytoplankton and rotifers while

seemingly not reducing larger-bodied cladocerans and copepods significantly, their presence may prove beneficial in improving water clarity. Lakes with high aesthetic goals such as water clarity, where high fish biomass may be of secondary concern, should consider encouraging the use of these exotic populations where they are already established to achieve their goals.

Conclusion 4. Turbidity (an assortment of particles) and phytoplankton were significantly lower in the clam-containing microcosms and these food deprivation may have caused significant mortality of larval fish.

Because of significantly lower amounts of food available to larval fish, it seems that fish larval mortality may have been caused by *Corbicula*'s ability to remove small particles from the water column. Results reported in Chapter 4 suggests that after larvae had absorbed their nutritional yolk sac, they were unable to find suitable food necessary for survival in microcosms containing *Corbicula*.

Conclusion 5. *Corbicula* extract large amounts of small particles (bacteria, phytoplankton, rotifers) from the water column and deposit these particles onto the substrate encased in a protein mucilaginous sheath.

It was shown in Chapter 5 that Corbicula have the ability to extract large amounts of small particles from the water column and to package these particles in a mucilaginous sheath onto the substrate. Phytoplankton cells encased in these sheaths are alive and stay that way for a couple of weeks.

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BIOGRAPHICAL SKETCH

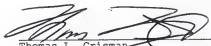
Robert J. Brock was born in Baumholder, Rheinland-Pfaltz, Germany in 1955. At age two, Robert moved to Provincetown, Cape Cod, Massachusetts, attended local schools, and graduated from Provincetown High School in 1973. He entered the University of Massachusetts (Amherst) in 1973 and transferred to Florida International University (Miami) in 1976 where he later was awarded a Bachelor of Science degree in Environmental Studies. Robert entered the Nova University Oceanographic Center (Dania) in 1985 where he later received a Master of Science degree in Marine Biology. In 1989, he entered the University of Florida and was awarded his doctorate in Aquatic Ecology in 2000.

Robert has been employed by the U.S. Government for most of his adult life. Between 1979 and 1992, he was employed by the U.S. Geological Survey's Water Resources Division in Atlanta (GA), Boston (MA), Miami (FL), and Ocala (FL). From 1992 until April 1994, he was employed as a Marine Biologist by the U.S. Army Corps of Engineers, Environmental Branch, Jacksonville (FL).

Beginning in May 1994, and continuing to present, Robert became a Supervisory Marine Biologist in the Marine Resources Program for the U.S. National Park Service's South Florida Natural Resources Center in Homestead, Florida.

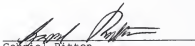
Between 1990-1992, Robert was an Adjunct Instructor in the Environmental Science Program at Santa Fe Community College in Gainesville (FL). In 1993, he served as an Adjunct Instructor in the Marine and Environmental Science Programs at Jacksonville University (FL).

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Thomas L. Crisman
Professor of Environmental
Engineering Sciences

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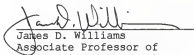
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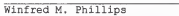


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Fisheries and Aquatic
Sciences

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